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A MONOGRAPHIC STUDY OF THE FERN GENUS ANEMIA, SUBGENUS COPTOPHYLLUM

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ABSTRACT. Morphological investigations in the fern genus Anemia, subg. Coptophyllum on both the sporophyte and gametophyte generations are discussed. The results and conclusions of the comparative research are summarized in a diagram showing the probable evolutionary relationships of the subgenera of Anemia and the genus Mohria. Species relationships within subg. Coptophyllum are postulated in a similar chart. A taxonomic revision of the subgenus is presented, including keys, descriptions, illustrations, and discussions of the taxa.

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INTRODUCTION

The Schizaeaceae is a primitive family of leptosporangiate ferns including the four genera Lygodium, Schizaea, Anemia, and Mohria. The genus Anemia is the largest of the four and is composed of about eighty species, which are widespread in Latin America, Africa, and southern India. It is readily recognized by the basal pair of pinnae being fertile, erect, and lacking a conspicuous lamina. These peculiar fertile structures make it well-known to morphologists; the structures resemble the controversial fertile spike of the Ophioglossaceae which is commonly considered to be the result of fusion of two fertile pinnae. However, the similarity is only superficial, for there is no relationship between the two families.

The genus Anemia has a richer fossil history than most living genera of ferns. It is known not only from leaf impressions, but also from distinctive fossil spores. They have been found to be important in stratigraphy, with the result that petroleum geologists have shown considerable interest in the study of modern Anemia spores.

Living plants of Anemia were popular in cultivation in England during the nineteenth century. Twenty-five species of the genus were listed by Schneider (1892) in his Book of Choice Ferns. Other than the above, the only practical use I have found attributed to Anemia was in John Smith's comment (1854) that a poultice made from Anemia seemannii was used by the women of Panama to induce abortion.

In the last one hundred years Anemia has been a popular subject for morphological study. The work on the genus Anemia, however, has been largely concerned with its taxonomy. The naked fertile panicles bear some resemblance to the differentiated fertile pinnae of Osmunda, and it was in this genus that Linnaeus (1753) placed the seven species of Anemia known to him. This treatment was followed by later authors (Savigny, 1797; Cavanilles, 1801) until Anemia was recognized as a distinct group by Bernhardi (1806), who described it as the genus Ornithopteris, but mentioned only two species. Some months later Swartz (1806) described it again, giving it the name Anemia and including in it seventeen species. Subsequent authors apparently overlooked Bernhardi's genus, for the name Anemia was generally accepted. The name Anemia was conserved by the Eighth International Congress in 1954 (Pichi-Sermolli, 1954b).

Swartz based the name of his genus on a misspelling ("anemon") of the Greek word for naked, referring to the naked fertile spikes; Kaulfuss (1824), however, noted the correct spelling of the Greek word was "aneimon" and accordingly changed the spelling of the genus to Aneimia.

The affinities of Anemia to other genera were noted by Swartz. He placed it with Lygodium, Schizaea, Mohria and some other primitive fern genera, in the order Spurie Gyratae, based on the nearly apical annulus of the sporangium. Kaulfuss (1827) segregated the genera Anemia, Lygodium, Schizaea and Mohria in a separate family, Schizaeaceae, and this treatment has been accepted by most botanists since then.

As more species were described and more diversity within the group was noticed, certain species or species groups were removed as separate genera. In 1842 Gardner erected the genus Trochopteris on the basis of the small, rosette-forming Anemia elegans (1842a), and an additional genus, Coptophyllum, to accommodate two species with greatly reduced lamina and dimorphic fronds (1842b). At the same time John Smith segregated the net-veined species of Anemia as the genus Anemidictyon (1842) and transferred Gardner's two species of Coptophyllum and two other species with dimorphic fronds to the genus Mohria (1843) on the basis that the fronds were either fertile or sterile and were not just partially differentiated.

A move was made toward reunion when Presl (1845), brought together the fragments except for Anemidictyon, combining Trochopteris, Coptophyllum, and Anemia and making two subgenera of Anemia: subg. Coptophyllum to include those species with dimorphic fronds and subg. Euanemia to include the remainder of the genus. This was the first use of the subgeneric rank within the genus.

John Smith (1854) founded the genus Anemiorrhiza on A. adiantifolia, and an additional satellite genus, Anemiaebotrys, was described by Fée (1869) on the basis of A. aspera, a species with fertile pinnae held horizontally.

The greatest stride in the taxonomic history of Anemia was made by Prantl (1881) in his comprehensive monograph of the entire family Schizaeaceae. He was the first to recognize the natural relationships of the species and to express them as subgenera and sections. There has been no more recent critical revision of the genus, and in the intervening period the number of species described for Anemia has increased greatly.

For example, Prantl's section Tomentosae, which included nine species in 1881, would now embrace thirty-three species. Most of the new species have been due to more extensive exploration, but some are due to splitting of Prantl's species.

With the many new species and the recognition of diversity of species within the sections, the incentive for splitting Anemia into separate genera was again great. Reed (1948) made three genera from Anemia, elevated the four usually recognized genera of the family Schizaeaceae to familial rank (Anemiaceae, Lygodiaceae, Mohriaceae, and Schizaeaceae), and made the family an order, Schizaeales. Further comment on this treatment will be made below. In the present revision, Anemia is considered as a single genus composed of three subgenera, Coptophyllum, Anemiorrhiza, and Anemia.

The subgenus Coptophyllum is divided into six sections and includes thirty-eight species and six varieties. Although most of the species are quite distinct, there are a few which are taxonomically confusing. Christ (1897) sums up the situation when he says, "Die Arten veriiren sehr und sind schwer absugrenzen." The great range of variation within individual species and the processes of subtle speciation, expecially in the section Tomentosae, have caused endless difficulties. A note on a herbarium specimen warns, "It will take long years of field work to distinguish the Brazilian species of the tomentosa group!" To a certain extent this is true, for it is usually difficult to distinguish ecological from genetic variation on the basis of herbarium specimens. Nevertheless, I have been able to detect a number of patterns of variation without extensive field work through an investigation of a greater array of characters than previous workers had exploited, and by the use of current improvements in the techniques and concepts of taxonomy.

My work is concentrated on the American species, in part because these are ones which are the most confusing, and in part because the African species have been so poorly collected. A number of problems are yet to be solved, some of them newly uncovered in the present research, and these will be pointed out in the taxonomic revision.

The close relationship of Anemia to Mohria, a genus of three species in southeastern Africa and Madagascar, has long been recognized. In fact, in many respects subg. Coptophyllum resembles Mohria more closely than it does the other two subgenera of Anemia. The two genera might best be considered congeneric, and for this reason I have brought Mohria into the study in several places.

MATERIALS AND METHODS

About 6500 herbarium specimens were borrowed, including nearly 3000 of subg. Coptophyllum. These were the principal basis for my research and were supplemented by study of living plants in Mexico and transplants in the University of Michigan Botanical Gardens.

Microscopic features of the lamina were studied from leaf clearings. Dried leaf segments were placed in 5% aqueous NaOH solution for one to four days, bleached with Clorox solution, and stained with tannic acid-ferric chloride in 50% alcohol, a modification of Foster's technique (1934). The stained segments were mounted in diaphane or piccolite.

Cross sections of the stipe were made on the freezing microtome at thicknesses of 25-50 μ and stained with 1% safranin and 0.5% fast green. Sections of the rhizome and root were made by hand and stained with a phloroglucinol-HCl solution.

Chromosome counts were obtained chiefly from the spore mother cells of young sporangia by the squash technique. Immature fertile pinnae were killed and fixed in Newcomer's Fixative (Newcomer and Brant, 1954) and stored in a refrigerated room at 40°F until studied. Somatic counts were obtained from root tips: these were removed from living plants and kept in a saturated aqueous solution of paradichlorobenzene in the cold room for four hours to kill the tissues and shorten the chromosomes. Then they were transferred to Newcomer's Fixative and stored in the cold room until needed. The root tips were hydrolyzed in 10% HCl for 10 minutes, stained with acetocarmine and squashed.

Spore studies were based chiefly on cleared spores. Some spore preparations were made by the acetolysis technique and mounted in glycerine jelly. However, the spores were frequently swollen from their normal size and shape, so measurements of these were found unreliable. Most spores were placed in a drop of 85% lactic acid with a cover slip and heated on a warming plate for several hours until the oil droplets had been driven out. These, and spores mounted in diaphane, kept their original size and shape most closely.

In order to study wall structure of the spore, sections were made on the freezing microtome. The spores were first stained on a slide with a 1% crystal violet solution. Gum arabic was added and the mixture was painted onto the stage of the freezing microtome. Although the blade was set for 5-μ sections, many of the spores were removed entire from the frozen matrix by friction of the blade. Enough thin sections were found, however, to show the major features of wall morphology. The sections were mounted in diaphane.

Viable spores for gametophyte studies were obtained from living plants at the University of Michigan Botanical Gardens and from a few dried specimens. Various media were used for germination. These are discussed in the text on gametophytes.

Drawings of spores, chromosome squashes, spore germination stages, and sex organs were made with the aid of the camera lucida. All other drawings were made under a microprojector.

MORPHOLOGY AND ANATOMY

The anatomy of the schizaeaceous ferns was studied by Prantl (1881) and described in detail by Boodle (1901). The morphology and anatomy of subg. Coptophyllum has not previously been treated. The bulk of research on Anemia has been on A. adiantifolia and A. mexicana of the subgenus Anemiorrhiza and on A. phyllitidis of subgenus Anemia. Although neither Boodle nor Prantl reports directly on species of subg. Coptophyllum, my studies have shown no great differences in internal anatomy between it and subg. Anemia.

Root

In species of subg. Coptophyllum a fibrous root arises from the stem at the base of each leaf. The diameter of the root varies from 0.2 mm to 1 mm, and the proportions of the internal tissues vary accordingly. The root cortex of A. karwinskyana with a root diameter of 1 mm, for example, was found to be 10 to 12 cells thick, whereas that of A. tomentosa var. australis with a root diameter of about 0.6 mm has a root cortex 6 to 8 cells thick. Boodle (1901) reports a cortex with a thickness of 12 cells or more in A. phyllitidis. The cortical cells are very thick-walled throughout in subg. Coptophyllum in contrast to those of A. phyllitidis. The latter has a thin-walled outer cortex grading into a sclerified inner cortex (Boodle, op. cit.).

The endodermis is many cells in circumference, in contrast to the few cells in that of Lygodium (Boodle, op. cit.) (Pl. I, Fig. A). The pericycle is one cell layer thick, and the xylem has the usual diarch condition, often with two very large tracheids in the metaxylem. A cluster of 3-5 protoxylem elements is found at each side of the xylem strand.

Boodle found the root of Mohria to be quite similar to that of Anemia. The only difference he reports is that Mohria lacks the two large tracheids in the metaxylem, the tracheids, rather, grading into larger, fairly numerous ones in the center.

Rhizome

The rhizomes of members of subg. Coptophyllum are quite variable in outward appearance and habit, but their internal structure is similar throughout. In A. tomentosa the rhizome may be horizontal and somewhat creeping with internodes as long as 1.5 cm (Pl. XXVII, Fig. B). In this species I will describe the leaves as "scattered" in reference to their position on the rhizome. Most species have rhizomes which are horizontal with internodes seemingly absent and with leaves clustered at the apex, or "caespitose" (Pl. XIV, Fig. A). In only a few species, e.g., A. flexuosa, A. smithii, A. wightiana, and members of A. villosa, are the rhizomes oblique to nearly verticle (Pl. XVIII, Fig. A). These too have caespitose leaves and no internodes. The species of subg. Anemiorrhiza uniformly have slender, creeping rhizomes with scattered leaves, whereas those of subg. Anemia have horizontal or oblique rhizomes with internodes lacking. Variation in the proximity of the leaves in the horizontal rhizome of A. tomentosa seems to be due to environmental conditions and is not of great comparative significance because the scattered leaf condition is found randomly in Mexican specimens. Specimens with scattered leaves, however, have been most frequently collected in the region of Paraguay and southern Brazil.

The leaf arrangement is polystichous, as it is in most of the genus, with a phyllotaxis of 2/5 (Prantl, 1881). However, subgenus Anemiorrhiza, which differs in so many features, also differs in having a strictly distichous leaf arrangement.

The rhizome branches frequently, in a monopodial fashion. Although branching does not seem to be related to leaf axils, it is difficult to

evaluate bud position because of the proximity of the leaf bases to one another.

The rhizome is clothed with long, multicellular hairs the color of which is characteristic. These are usually orange or maroon. What I shall call "orange" refers to a hue of orange-orange-scarlet, value of about 13, and degree of about 12 in Villalobos' Colour Atlas (1947); "maroon" refers to a hue of scarlet-scarlet-orange, value of about 5, and degree of about 12. The hairs consist of several elongate cells with the small, terminal cell apparently glandular (Pl. II, Fig. C_1). No secretion was found on these cells either in the fresh or dried condition, but their smaller size and thinner walls in contrast to the subtending cells and their differential staining (red with safranin while subtending cells take fast green) lead me to conclude that the tip cells are glandular. These and other presumably glandular hairs on the leaf may produce the odor reported for A. tomentosa by Savigny (1797), "elle exhale une odeur aromatique fort analogue a celle de la myrrhe." Personal communication from E. R. de la Sota and notes on two herbarium sheets have also pointed out the odor in this species.

A cross section of the rhizome shows the stem to be dictyostelic ("dialystelic," Boodle, 1901). The vascular bundles are imbedded in a matrix of very thick-walled and elongated (2-6 times as long as broad) cells, which compose the major volume of the stem. These cells do not appear sclerified, and there is no differentiation of a truly sclerified inner cortex as in subg. Anemiorrhiza.

In addition to the specifically stelar bundles, a number of leaf traces are evident in a cross section (Pl. I, Fig. F). Internal to each of these is the remarkable space so peculiar to two of the subgenera. A slender pocket, an extension or invagination of the leaf axil, runs all the way into the pith of the stem (Pl. I, Figs. C, E, F). The leaves are decurrent along the stem, and the leaf axil continues into the rhizome for a distance of nearly 1 cm. The pocket is densely lined with short, multicellular glandular hairs (Pl. I, Fig. D), which are like an abbreviated form of those that cover the outer surface of the rhizome. The glandular tip cells of the "pocket hairs" are larger than those that cover the external surface. Since these pockets are associated with the leaf traces, their number in a single section varies according to the separation of the leaves on the stem; there may be as few as one or two per section in some forms of A. tomentosa with creeping rhizomes, or as many as ten as in A. villosa, which has no apparent internodes.

An individual bundle of the stem stele is surrounded by an endodermis, and a pericycle which is usually one cell thick. The xylem is a flat band of scalariform tracheids with scattered parenchyma, which more or less follows the outline of the bundle as a whole. The phloem forms a layer, which is continuous on the adaxial side of the xylem, but more irregular and often discontinuous on the abaxial side with parenchyma intermingled with the sieve cells. The phloem is separated from the xylem by a layer of "conjunctive parenchyma" (Boodle, 1901), one or two cells thick.

In progressively more apical sections, the first sign of the departure of a leaf is the appearance of the leaf-axil pocket on the inner side of a vascular bundle of the stele (Pl. I, Fig. F). At this stage the pocket is small and circular. A root trace departs from the bundle, usually near

one end or the other, and the bundle itself soon breaks into three portions (Pl.I, Figs. F_1-F_3). The band in the center departs to become the leaf trace, the lateral round bundles continue as part of the stele. The lateral bundles may be cylindrical or ribbon-shaped. The leaf trace and axillary pocket depart gradually through the cortex, the trace becoming tangentially flattened and the pocket assuming a triangular shape and then becoming laterally broad and flat before opening on the outside of the rhizome (Pl.I, Figs. E_4, F_6).

The lateral bundles remain within the rhizome, each one of them soon uniting with the bundle nearest to it to form a new arch (Pl.I, Figs. F_3, F_6), which in turn will divide into a root trace, leaf trace, and two stelar bundles.

The vascular trace leading to a branch of the rhizome arises from one of the stem bundles as shown in Pl.I, Figs. F_4-F_6. The branch stele begins as an unbroken cylinder. A root trace emerges from one side of the cylinder, and a leaf trace from approximately the opposite side. The latter creates a leaf gap (Pl.I, Figs. E_1-E_4). The resulting horseshoe-shaped stelar bundle has a slight tendency to close, but before it does, another root and leaf trace form that now dissect the stele into a dictyostele. Further rhizome branch growth remains dictyostelic, and follows the pattern described above for the parent stem.

The stem anatomy of Mohria is almost identical to that of Anemia except for the lack of axillary pockets (Boodle, 1901).

Leaf

Habit

In general, the frond is petiolate and erect in subgenus Coptophyllum. It ranges from 15 to 60 cm tall. The division of the frond is usually bipinnate to tripinnate, but the variation is great, ranging from once pinnatifid to tripinnate-pinnatifid. The sporangia are borne on the lowermost pair of pinnae, which are usually held erect. In other respects the fronds are nearly isomorphic.

In the section Coptophyllum, however, two species are outstanding in their extreme reduction of lamina and in their complete dimorphism of fertile and sterile fronds (Pl. XV). The significance of dimorphism will be discussed later.

The two species of section Trochopteris, A. elegans and A. eximia, are peculiar in their formation of flat rosettes on the ground (Pl. XVIII, Fig. B; Pl. XIX, Fig. A). Anemia elegans is extremely small and compact, the fronds being only simply pinnatifid. Although A. eximia forms a rosette, in several respects it represents an intermediate step between section Trochopteris and the more generalized types of subg. Coptophyllum.

Petiole

A cross section of the petiole is deltoid in shape with rounded corners and may be shallowly to deeply sulcate on the adaxial side (Pl.I, Fig. B). The epidermis and cortex are heavily sclerified in the outermost six to eight layers of cells, grading into a thin-walled inner cortex six to ten cells thick.

The vascular bundle that serves the petiole changes in shape somewhat as it passes through the cortex. It changes in cross section from a flattened arch to a V. The xylem follows the outline of the bundle but has inwardly hooked ends. In A. (subg. Anemia) pastinacaria the hooks are very slight and inconspicuous if present at all, but usually they are more fully developed. There are three protoxylem groups: one at the apex of the V and the other two inside the hooked ends. According to Boodle (1901) only the central group contains spirally thickened tracheids, the others being strictly scalariform pitted.

The phloem surrounds the xylem on the abaxial side and half-way up the adaxial surface of the xylem arms. It is separated from the xylem by a 1-2 celled layer of "conjunctive parenchyma." It is narrowest at the top of the arch and around the ends, and it is in these areas that phloem elements become lignified fibers in some species. This is true in A. raddiana and A. villosa (subg. Coptophyllum); A. phyllitidis, A. underwoodiana, A. rotundifolia (subg. Anemia); and A. adiantifolia (subg. Anemiorrhiza). Phloem fibers are lacking in A. tomentosa var. anthriscifolia (subg. Coptophyllum), A. pastinacaria (subg. Anemia) and Mohria.

The endodermis is distinct, one cell layer in thickness, and the pericycle completely surrounds the vascular tissue in a layer one to four cells thick.

In his studies of fern leaf traces, Sinnott (1911) proposes that "in every case the simplest and most primitive structures and relations of the vascular system occur at the node or in the base of the leaf trace." He points out a similarity between the Schizaeaceae (Anemia) and the cheilanthoid ferns in that the trace is more or less deltoid with three protoxylem points. The trace of Pellaea atropurpurea resembles that of Anemia quite closely. Bower (1928) reports additional resemblances of the vascular tissues of Cheilanthes and Pellaea to those of Anemia.

Externally the stipe displays a number of features which have comparative value. The stipe is very short in A. elegans and is up to 55 cm long in A. aspera. Within a given species, however, there is considerable variability besides the usual variation in plant size. Although the blade of a sterile leaf is usually larger than that of a fertile one, the sterile leaf as a whole is shorter because of its shorter petiole (Pl. XXX, Fig. A).

The stipe is semiterete and sulcate on the adaxial side in most species. A strongly flattened stipe and rachis has occurred independently in A. aethiopica, A. perrieriana, A. retroflexa, and the section Pachypoda. In these species the axis is flattened dorsiventrally with a deep furrow on each side. A close relative of A. aethiopica, namely A. schimperiana, shows a tendency toward this condition, but it is not pronounced or consistent. In a number of other species, such as A. flexuosa, A. villosa, and A. aspera, the stipe may be somewhat flattened at the base.

The stipe is usually slender, being 1 mm broad or less (measured midway on the stipe) in A. tomentosa var. australis, A. smithii, and A. simii. On the other hand, some species have a stout stipe about 2 mm in breadth (A. flexuosa, A. raddiana, A. angolensis, A. imbricata), and up to 2.5-3.0 mm in the flattened stipes of A. lanipes and A. retroflexa.

The surface color of the stipe is usually a dull yellow-orange or light brown in dried material. Some species, however, have different colors. Several have a bright yellow stipe, even after drying, such as A. karwinskyana, A. angolensis, and A. simii. On the other hand, A. ferruginea is noted for its deep wine color, and it was once named A. rubrostipes. The stipe color of A. ferruginea is variable, however, that of some specimens being light yellow.

The amount of indument on the stipe is another variable feature of these plants. Although most plants are moderately hirsute with reddish-orange hairs, some species are conspicuous for their abundance or paucity of hairs. Anemia aethiopica and A. wightiana have abundant orange hairs. Several smaller species, such as A. trichorrhiza and A. myriophylla, are lanose. The hairs of A. myriophylla are nearly white in many specimens. The stipe of A. flexuosa typically has stiff black hairs. A. ferruginea, though variable, is usually nearly glabrous; thus with its dark stipe, it resembles many cheilanthoid ferns.

Blade

Segmentation. The blade in the species of subg. Coptophyllum is usually 15 to 60 cm tall, but measurements outside these limits are found; the abbreviated A. elegans bears fronds as small as 1 cm, whereas A. aspera reaches a meter in height.

The outline of the blade is generally deltoid-ovate. Only in the more specialized taxa is it subovate (A. tomentosa var. tomentosa, Pl. XXVII, Fig.B), or linear-ovate (A. villosa, Pl. XXIII, Fig.A). Some taxa attain a strictly deltoid outline (A. tomentosa var. anthriscifolia, Pl. XXVIII, Fig. A).

Division of the blade is various: tripinnate to tripinnate-pinnatifid (A. colimensis), bipinnate-pinnatifid (A. guatemalensis, A. aspera), once pinnate (A. organensis, A. blechnoides), and pinnatifid (A. elegans). Most species, however, are bipinnate to bipinnate-pinnatifid.

Variation in shape and dissection of the segments is illustrated in Pl. II, Fig. A. The segments are usually adnate to the costa and borne obliquely. Their shape may be elongate-obtuse (A. smithii), deltoid-obtuse (A. ferruginea var. ferruginea), ovate (A. karwinskyana), or lanceolate (A. ferruginea var. ahenobarba). The segment base tapers in most species, but is subcordate in the A. karwinskyana group.

The segments are rarely completely unlobed (some specimens of A. organensis and A. raddiana). More often they are coarsely crenate, lobed, or pinnatifid. The lobes are either obtuse, acute, or rarely acuminate. The margin is smooth except in the two most primitive species, A. aspera and A. perrieriana, which are dentate with a single vein ending in each tooth. This condition is also found in Mohria. Apparently this was the condition of the common ancestor of the two genera and can be considered the primitive condition in Anemia.

Segment size is largely a reflection of the degree of dissection of the leaf and the size of the plant. Two small species, A. myriophylla and A. madagascariensis, which are nearly tripinnate, have segments which are only 2 mm long and 2 mm wide. A larger tripinnate species, A. colimensis, has segments about 5 mm long and 5 mm wide. Anemia smithii, a small, bipinnate species, has segments about 8 mm long and 4 mm wide, whereas larger taxa of like dissection (A. raddiana, A.

flexuosa, A. tomentosa var. australis) have segments about 15 mm long and 8 mm wide.

Lamina. The texture of the lamina is usually chartaceous, but a number of species are quite coriaceous. An intermediate condition is found in A. tomentosa var. tomentosa and some other taxa.

Laminar pubescence is a distinctive feature in some cases. The usual condition is pilose to hirsute on both adaxial and abaxial surfaces. Most of the coriaceous species, however, are subglabrous above and subglabrous to pilose below. Anemia trichorrhiza is only slightly pubescent above but so densely lanose below it is difficult to see the epidermis at all in leaf clearings. Anemia myriophylla, on the other hand, is lanose on the entire blade. In addition to the conspicuous multicellular hairs, the blade is provided with numerous unicellular hairs.

Venation. The ultimate veins in the leaf segments are free, usually once to several times forked, the branches unequal (Pl. II, Fig. D_1). Only in A. X ulbrichtii are the veins anastomosing, but this condition is due to hybridization of A. (subg. Coptophyllum) raddiana with A. (subg. Anemia) phyllitidis (Pl. II, Figs. D_2, D_3). The latter belongs to sect. Anemia, the only section in the genus with the veins sometimes anastomosing.

Of the plants which are once pinnate, A. organensis and A. blechnoides have a strong midrib, as a rule, with the vein systems running from it to the margin (Pl. II, Fig. D_5). In contrast, A. gardneri and A. lanuginosa are flabellately veined with no midrib whatsoever (Pl. II, Fig. D_6).

Pinnule position. The position of the acroscopic and basiscopic pinnules in relation to each other are important variables. The terms "anadromous" and "catadromous," as usually understood, do not quite apply to the situation in Anemia, however. These terms refer, according to most definitions, to the origins of the first pinnules (or veins) on the pinnae. Anadromous pinnae are those in which the first pinnule is the acroscopic or distal one; catadromous pinnae are those in which the first pinnule is the basiscopic or proximal one. In Anemia, the first pinnules are usually more or less opposite—it is the next pair of pinnae and to a greater or lesser extent those which follow, which show characteristic positions. So far as I have been able to determine, when Prantl (1881) used the terms anadromous and catadromous he was actually referring to the relative pinnule positions beyond the first pinnule pair. Since there are no other terms available for the condition that characterizes Anemia, I shall continue to use these terms in Prantl's sense, but with the understanding that the first pinnule pair should not be considered in deciding whether or not the pinna is anadromous or catadromous. The second, third, and fourth pinnule pairs are the ones which show the contrasted conditions.

The pinnae are anadromous at the base of the frond and catadromous at the apex. In most species the pinnae are dominantly anadromous, the transition to the catadromous condition taking place in the upper third of the leaf (Pl. XII, Fig. A). But in the A. karwinskyana group, and occasionally in A. aspera and A. perrieriana, the pinnae are largely catadromous, the transition occurring in the second or third pinna pair from the base (Pl. XXXII, Fig. A).

Mesophyll. There is some differentiation of the mesophyll into palisade and spongy tissue. The degree of this differentiation depends, at least in part, on the texture of the leaf. Coriaceous leaves, such as those of A. ferruginea, have less differentiation, the lower cells being tightly packed and with only small air spaces; A. elegans has only spongy mesophyll; A. madagascariensis, A. simii, and A. sessilis have only palisade. A few species, such as A. aspera and A. organensis have extremely large air spaces among the spongy cells as well as having palisade.

Epidermal cells. There is much variation within the subgenus Coptophyllum in the pattern of their epidermal cells. On the same plant the cells of the lower epidermis are generally more convoluted or with more rounded arms than are those of the upper epidermis. From the standpoint of comparison of species, this is of limited value, but certain trends can be seen. The fundamental and most common cell pattern seems to be one of irregular cells on both the abaxial and adaxial surfaces (Pl. III, Fig. B). This condition is found in most species of subg. Coptophyllum as well as in the genus Mohria.

In some species there has been a modification of the upper epidermis to cells that are much more slender and regular with wavy walls (Pl. III, Fig. B_2). This is the rule for members of the section Pachypoda, and has arisen independently in A. madagascariensis.

Another apparent trend has been toward cells whose lobes are square-oblong (Pl. III, Fig. B_3). This is characteristic of the section Adetostoma and A. flexuosa.

In contrast to these trends toward less irregular epidermal cells, the group of A. simplicior, A. raddiana, and A. bartlettii have cells with rather long, slender arms (Pl. III, Fig. B_4). The most extreme example of contorted epidermal cells is found in A. elegans, which displays an amazingly intricate pattern of sinuous-armed cells (Pl. III, Fig. B_5).

Epidermal cells are notably subject to changes with environment, but in Anemia the consistency of general features, such as the contorted epidermal cells, enables us to use these features in establishing certain broad relationships.

The walls of epidermal cells vary in thickness (double wall thickness) from less than 1 to nearly 6 μ (Pl. III, Fig. B_2). This reflects, to some extent, the texture of the leaf. The entire section Pachypoda has thickened walls, while A. ferruginea, most of A. flexuosa, and some specimens of A. tomentosa share this character.

As is usual in leaves in general, epidermal cells covering the veins are extremely slender, much longer than other cells, and with straight to only slightly wavy margins.

Marginal cells and spicules. The margin of the leaf is bounded by elongate cells differentiated from the others, the marginal cells in one, or occasionally two or three rows. Their outer walls are generally smooth, but in a few species they are ornamented with numerous small spicules (ca. 4 μ high with a basal diameter of ca. 7 μ) (Pl. II, Fig. B). With some care, they are observable under the dissecting microscope (45X). These are a characteristic feature in A. ferruginea and in most species of sect. Coptophyllum, and are found occasionally in A. glareosa and A. tomentosa vars. anthriscifolia and tomentosa. They have also

been observed in some specimens of A. flexuosa, especially those from Colombia. When they are not abundant on a plant, they are found only in the margin of the sinuses. The leaves of these plants are somewhat coriaceous, and their epidermal cell walls are at least slightly thickened. Therefore, marginal spicules seem to be correlated with coriaceous texture and perhaps a xeric habitat. They are lacking, however, in the species of section Pachypoda, all of which have coriaceous leaves.

Stomates. The stomates are borne on the abaxial surface of the leaf except in A. elegans, which has its stomates on the adaxial surface. This undoubtedly is correlated with its small, compact, flat rosette habit. The stomates in all species are elevated somewhat above the epidermal cells. Each stomate is located at the distal end of an epidermal cell, the subsidiary cell, and nearly surrounded by it (Pl. III, Fig. A_1), so as to appear to be affixed to the wall of the subsidiary cell. The subsidiary cell is generally more nearly isodiametric than the other epidermal cells.

A more unusual position for the stomates in Anemia is to be "suspended" by a presumably double wall from the distal, or rarely the proximal, wall of the subsidiary cell (Pl. III, Fig. A_2). This condition is apparently derived from the "affixed" stomate by complete surrounding of the stomate by the subsidiary cell in the maturation of the leaf. It occurs only in the section Coptophyllum of this subgenus, but is common in subg. Anemiorrhiza.

A third position for the stomates is "floating" in the center of the subsidiary cell with no attachment whatsoever to a lateral wall (Pl. III, Fig. A_3). The stomatal aperture, however, does connect with the mesophyll air spaces below. The only groups in subg. Coptophyllum which have floating stomates are the sections Adetostoma and Coptophyllum. In the other two subgenera the floating stomate is much more common: several species of subg. Anemiorrhiza have floating stomates, and all members of subg. Anemia show this condition. Apparently the floating stomate has arisen independently a number of times in the genus Anemia alone. It is known from other fern genera as well, i.e., Platycerium and Pyrrosia (De Bary, 1884; Ogura, 1938). The ontogeny of the floating stomate is not known. In the nineteenth century, a number of German morphologists traced it, but their explanation of it by the formation of a funnel-shaped wall has not been entirely satisfactory.

In the species of subg. Coptophyllum the stomates vary from 30 to 70 μ in length. Stomatal length varies greatly on a single leaf, stomates near the leaf margin being considerably smaller than those toward the center of the leaf. In a leaf of A. tomentosa var. australis, for example, stomatal length grades from 34 μ at the margin to 44 μ at the center of the pinnule. Comparison of stomatal lengths between species is based on samples taken midway between the center and margin of leaf segments.

Variation in stomatal length from species to species depends at least in part upon differences in ploidal level within the group. Because of a lack of cytological knowledge of most species, care should be exercised in arriving at conclusions. Some speculation regarding the ploidal levels in other species, however, can be based on the few chromosome counts which have been made. A comparison of stomatal and spore sizes in various species in regard to probable ploidal level is discussed in the section on Cytology.

Trichomes. The blade in all species is clothed with three kinds of trichomes, at least in the young stages of the development of a frond. The most obvious of these hairs are multicellular (two or more cells long). They usually consist of a short basal cell, three to six elongate cells, and a thin-walled, glandular, tip cell (Pl. II, Fig. C_1). Those of Anemia elegans and A. eximia consist of several cells or only one cell, and in A. elegans the smaller ones lack a glandular tip. A unique situation is found in A. colimensis: in addition to the usual multicellular hairs, which are in this species limited to the veins, the adaxial laminar surface has numerous stiff, very thick-walled, unicellular hairs (Pl. II, Fig. C_7), which are identical with those of A. elegans. The multicellular hairs of subg. Anemia are identical with those of subg. Coptophyllum, whereas hairs of subg. Anemiorrhiza differ in having an acuminate tip and no glandular cell.

In addition to the multicellular hairs, there are two types of thin-walled, unicellular trichomes, both presumably glandular. The larger of the two is generally linear-ovate and is attached subterminally to an epidermal cell (Pl. II, Fig. C_2). Hairs of this type are large enough to be seen with a hand lens or dissecting microscope. Usually their length is about three times the width (e.g., 98 x 33 μ, 130 x 35 μ). These trichomes are considerably longer in some species, such as A. aspera (up to 172 x 46 μ, Pl. II, Fig. C_3). On the other hand, certain members of the A. tomentosa complex (A. ferruginea and A. tomentosa vars. anthriscifolia and tomentosa, Pl. II, Fig. C_5) have ovate trichomes, the length usually being less than twice the width (e.g., 78 x 52 μ). Another modification of this type of trichome is the medial attachment found in Anemia simplicior (Pl. II, Fig. C_4). An attachment intermediate between the central and subbasal positions occurs in some specimens of A. raddiana.

The smaller unicellular hair differs in that it is attached terminally and is much smaller (32 x 14 μ to 70 x 27 μ, Pl. II, Fig. C_6). Its length seems to be correlated with that of the stomates, and hence reflects the ploidal level of the plant. This trichome is usually attached to an epidermal cell which differs from other epidermal cells in being smaller and less contorted.

Fertile pinnae

The most distinct feature of Anemia in general is its upright pair of fertile basal pinnae. These fertile spikes have greatly reduced leaf tissue. They may be longer or shorter than the sterile blade. Their height relative to the sterile blade is characteristic for certain taxa. In A. tomentosa var. anthriscifolia, A. ferruginea, A. simii, and A. raddiana, for example, the fertile pinnae are always long and slender, sometimes twice the length of the sterile blade (Pl. XXVIII, Fig. A). In other taxa such as A. flexuosa, A. tomentosa var. australis, A. karwinskyana, and A. guatemalensis, the fertile pinnae are shorter than or at least do not exceed the sterile blade (Pl. XXIX, Fig. A).

The fertile pinnae are tripinnate in nearly all species, regardless of the degree of dissection of the sterile lamina. Anemia organensis is only once pinnate while A. aspera is nearly tripinnate, but the fertile pinnae are tripinnate in both.

The segments of the fertile pinnae are linear and are served by one vein each. Although the lamina is greatly reduced, there is still a trace of it in subg. Coptophyllum; i.e., the segments are about 1 mm broad. The species of subg. Anemiorrhiza have a similar amount of lamina, whereas those of subg. Anemia lack laminar tissue altogether. The remnant of a lamina is taken to be a primitive feature of these subgenera, whereas the complete loss of lamina is apparently the derived condition.

Not only is the laminar tissue of the fertile pinnae reduced in width but also in thickness. In fact, the mesophyll is lacking, and there are only the two epidermal layers. Stomates are borne on the abaxial epidermis.

The fertile pinnae may be slender, as mentioned above, or short and "bushy," as in A. imbricata (Pl. XXIV, Fig. A). They may be densely pubescent or nearly glabrous. The degree of hairiness is useful in separating certain species: Anemia simii has glabrous fertile spikes, whereas A. angolensis, which is commonly confused with it, has densely pubescent fertile pinnae.

The erect fertile pinnae are considered to be modifications of normal pinnae on which the sporangia have become localized and later held erect. It was thought at one time (Gardner, 1842b) that the fertile frond was formed by fusion of the stipes of two fertile spikes and one sterile leaf. This was based on Gardner's idea that dimorphism as seen in Anemia (subg. Anemiorrhiza) aurita was the basic condition.

In A. aspera and A. perrieriana, the lowermost pinna pair is fertile, but held in the same plane as the sterile pinnae. In this position, they closely resemble the normal sterile pinnae, although thay are skeletonized. This is the most primitive condition found in Anemia today. An even more primitive stage would be for the entire frond to bear sporangia on the abaxial surface of normal, nonskeletonized pinnae. This condition is found in the genus Mohria.

There are several other species in which the fertile pinnae are either horizontal or suberect (A. sessilis, A. trichorrhiza, and the species of sections Trochopteris and Adetostoma). The similarity of unusual habit of the fertile pinnae in these species does not necessarily imply a close affinity among them, for on the basis of other morphological evidence their relationships are remote. In sect. Trochopteris the condition is probably secondary and associated with the reduced leaf size; in the others the condition is probably primitively retained.

Labouriau (1951b) has shown that the erect position is due to a negative geotropism during development and that the fertile pinnae are sites of hormone production. The development of growth hormone within the fertile pinnae, resulting in an upright habit, should be considered as a derived condition. The most primitive members of the genus bear their fertile pinnae in the same manner as the sterile pinnae. The erect habit may well have a selective advantage in raising the spores to a more effective position for wind dispersal. All those species holding their fertile pinnae in any other position, such as horizontal or suberect, are rare and local.

Teratologies. A number of teratological forms are found in which there is a varying degree of sterility of the fertile pinnae or fructification of the sterile pinnae. All transitional stages can be seen, e.g.,

basal pinnae sterile but more dissected than normal sterile pinnae, basal pinnae fertile only at the base or apex, and normally sterile pinnae fertile. Labouriau (1951a, 1951b, 1952a, 1952b, 1952c) and Goebel (1931) have made morphological studies and speculations on the significance of these teratologies.

Similar abnormalities have been found in many of the species examined (A. tomentosa, A. raddiana, A. simplicior, A. villosa, A. phyllitidis, A. mexicana). The name "forma transitoria" was applied by Rosenstock (1907) to those teratologies in "A. flexuosa" [A. raddiana] and A. phyllitidis, and this name has been applied to other species showing the same intermediate or abnormal structure. These are of morphological interest in showing irregularity in the relative fertility of the frond, but I do not believe that they deserve taxonomic recognition or designation.

Origin of the fertile pinnae. The point at which the fertile pinnae leave the stipe varies widely, but there are two basic positions. The primitive position is at a point remote from the lowermost vegetative pinnae, i.e., in what would be the normal position for pinnae if there were no differentiation of them into fertile structures (Pl. XXIX, Fig. A). This is the position seen in the most primitive species of the genus, and it agrees with current ideas on the origin of the fertile structures.

The alternative extreme is for the fertile pinnae to arise from the stipe at a point closely approximate to the lowermost sterile pinnae (Pl. XXVIII).

The position of the fertile pinnae is usually constant, not only for species, but also for subgenera. Thus, the subgenus Anemiorrhiza, which is primitive in a number of other characters, has its fertile pinnae typically in the remote position. On the other hand, the subgenus Anemia, the most specialized subgenus, with only two exceptions maintains its fertile pinnae in the approximate position. Subgenus Coptophyllum, however, is variable in this respect. A number of taxa, including A. tomentosa var. australis, A. aspera, and A. flexuosa, display the remote position consistently. In other taxa, such as A. ferruginea, A. simii, and A. tomentosa vars. anthriscifolia and tomentosa, the approximate position is the rule.

Discretion must be exercised, however, in using this character to distinguish species. In species which typically have the approximate position, occasional specimens are found showing the remote condition. Intermediate conditions are also frequently found, as in some specimens of A. ferruginea and A. villosa. In only a few species, however, such as A. lanipes, is the position of the fertile pinnae consistently intermediate.

Frond dimorphism

In all species of Anemia the fronds can be considered dimorphic in the sense that the fertile fronds differ from the sterile. In addition to differentiation of the basal pair of pinnae as fertile organs, the fertile fronds are usually taller, due to a longer petiole, whereas the sterile fronds have short stipes and frequently have larger blades.

In the genus Anemia the term "dimorphism" has been used in a restricted sense, referring to species whose fertile fronds bear sporangia

on all pinnae. This extreme form of dimorphism is rare in the genus and in subg. Coptophyllum occurs only in the section Coptophyllum. In two species of this section, namely A. millefolia and A. buniifolia, the fertile fronds are somewhat taller than the sterile and completely sporangiferous (Pl. XV). A third species of the section, A. rutifolia, displays an intermediate condition (Pl. XVI, Fig. A). Its sterile fronds are short, nearly sessile, as are those of A. millefolia, and A. buniifolia. The fertile fronds are much taller, with one to four fertile pinna pairs, the apex typically sterile. Characters of the spores and blade dissection in A. rutifolia are also intermediate between those of sect. Coptophyllum and the more generalized form of the subgenus. Anemia millefolia and A. buniifolia also vary in their degrees of dimorphism. Specimens of these species are frequently found with fronds only partly fertile, displaying the entire transitional series in some cases.

Although some species of subg. Coptophyllum are strongly dimorphic, in striking contrast to other members of the subgenus, the character of frond dimorphism should not be overemphasized by creating a separate genus or subgenus for it (e.g., Coptophyllum Gardner, 1842b). Dimorphism is common also in subg. Anemiorrhiza. The most abundant species, A. adiantifolia and A. mexicana, have isomorphic fronds, but half the species of this subgenus are dimorphic. Anemia abbottii, A. cicutaria, A. wrightii, A. aurita, and A. portoricensis are regularly dimorphic. In a Cuban species, A. coriacea, both conditions are known; the generally distributed isomorphic form is typical A. coriacea, but a dimorphic form known only from the Sierra de Nipe and otherwise identical with A. coriacea, has been called A. nipeensis. Apparently the differences here have been caused by a simple mutation, perhaps of a single gene or a few genes. Mixture of the two in a few populations could be due to segregation of the mixed genes of a heterozygote. Since the plants of these populations produce completely normal spores, there would appear to be no isolation barrier between the two, and hence they could best be considered varieties or forms of the same species, A. coriacea.

Although the change to dimorphism seems spectacular, in Anemia it is apparently a relatively simple and taxonomically minor one which has occurred at least twice in the genus.

Sporangia

The sporangia are borne on linear segments of the fertile pinnae in two rows, one on each side of the vein. In the development of the fertile pinnae, the remnant of a lamina is curved around the sporangia in a protective manner.

The sporangium is sessile, suberect, ovate-globose, and about 550 μ long and 430 μ broad (Pl. VI, Fig. C_1). its annulus is subapical, consisting of a single row of elongate, thick-walled cells, or "bow" (Wilson, 1958), and a stomium, and forms a ring around an apical plate of small cells (Pl. VI, Fig. D). The number of bow cells varies from 12 to 19. The length of the bow cells in relation to the length of the sporangium is distinctive in a few species. In Anemia buniifolia, A. millefolia, and A. elegans the bow cells extend nearly one-half the length of the sporangium, whereas the usual length is about one-fourth to one-third that of the sporangium.

The apical plate consists of 4 to 15 small cells. In most species of subg. Coptophyllum these cells have thick walls (Pl. VI, Fig. D), as they have in subg. Anemiorrhiza and the genus Mohria, whereas those of subg. Anemia are thin-walled.

The stomium consists of cells which are smaller and thinner-walled than those of the annulus. In subg. Coptophyllum the stomium is differentiated only in the area of the bow, but in the other two subgenera the stomium extends downward approximately half the length of the sporangium (Pl. VI, Fig. C_2).

The cells of the sporangium have straight or slightly irregular walls in Mohria and nearly all species of Anemia. In contrast, those of A. elegans are highly undulating (Pl. VI, Fig. C_3). Apparently this feature is related to its extremely contorted laminar epidermal cells.

The large, globose sporangium of Mohria (Pl. VI, Fig. C_4) is markedly different from that of Anemia. This is one of the few major features that keep the two genera distinct.

Spores

The spores of Anemia are distinct among the ferns in being both tetrahedral and in possessing a series of conspicuous parallel ridges separated by grooves or striae. The generalized spore of subg. Coptophyllum is large (usually 65-110 μ in diameter[1]) and tetrahedral-globose. The ridges are more or less parallel to each other and to the equator, anastomosing in the center of the distal side and at the angles of the tetrahedron, where short, wart-like protuberances are formed (Pl. IV, Fig. A). On the proximal surface there is a triradiate scar, the laesura, which is composed of a slender, elevated crest and a stria on each side. The laesura is bounded by a ridge to which are attached the rung-like ridges of the three proximal faces.

Three other fern genera have striate spores which resemble those of Anemia to some extent. Ceratopteris has no ridges immediately bordering the laesura and its ridges do not anastomose at the angles in the same way as in Anemia (Pl. IV, Fig. B). The spores of Schizaea are strictly bilateral rather than tetrahedral. Mohria has spores which are nearly identical with those of such species as A. simii and A. simplicior (Pl. IV, Fig. C). Although it is sometimes difficult to distinguish Anemia and Mohria on the basis of their spores, those of Mohria can usually be told by the light, apparently hollow area down the center of each ridge. This feature will be discussed below.

The spores of subg. Coptophyllum are relatively large for Anemia (usually 65-110 μ in diameter). The ridges are broad (3-6 μ wide), relatively smooth, and with narrow striae (1-4 μ, not exceeding the width of the ridges). The wall is usually about 7 μ thick.

Spores of the other two subgenera are similar in having the more or less parallel ridges and triradiate crest, but they are distinct for the most part. Most species of subg. Anemiorrhiza have thin-walled, "hollow," undulating ridges, with striae broader than the ridges and no protuberances at the angles (Pl. IV, Fig. D).

[1] Spores were measured across their greatest equatorial diameter, not including the angle protuberances.

In subg. Anemia the spores are thin-walled and have very slender ridges which are usually beset with "spines" or clavae (Pl. IV, Fig. E). This condition is nicely exemplified by the well-known species A. phyllitidis. In sect. Hirsutae, however, the spines are lacking, leaving only the slender ridges with their broad striae. Spores of sect. Oblongifoliae are broad-ridges with narrow striae, thus resembling subg. Coptophyllum. Several transitional types are found between the smooth ridges of A. hirsuta and the spiny ridges of A. phyllitidis. Anemia dregeana of South Africa possesses slight bumps on its ridges, and A. pastinacaria displays all stages of transition from smooth ridges to long "spines." This transitional phase is an interesting one from the standpoint of spore morphology and the evolution of this spore type within Anemia.

Within subg. Coptophyllum itself there is great diversity in spore morphology. The majority of species have spores which are tetrahedral-globose. From a polar view the spores appear more or less triangular, the angles being punctuated by short protuberances derived from the meeting of the ridges at the corners, and the sides of the spores convex. In a few species, such as A. aspera and A. organensis, and in some specimens of A. villosa, the sides are nearly straight, giving the spore a triangular shape (Pl. IV, Fig. F). In this type of spore, the angle protuberances are much more prominent than usual. On the other hand, in such species as A. millefolia and A. perrieriana, the spores are nearly globose, the angle protuberances being much less conspicuous.

Certain species have spores with rounded angles, the angle protuberances inconspicuous or lacking altogether. This is well illustrated in A. madagascariensis, A. aethiopica, and the A. karwinskyana group (Pl. IV, Figs. G, H, I, J).

As mentioned above, the ridges of the proximal faces are arranged parallel with the equator, but there is some deviation from this condition. These ridges may be somewhat angled and almost parallel to one of the arms of the laesura (Pl. IV, Figs. G, H, J). This occurs occasionally in several species but regularly in A. guatemalensis and A. madagascariensis.

In several species of sect. Tomentosae the walls of the ridges are slightly warty, or verruculate. In some species, such as A. karwinskyana and A. tomentosa, the ridges have only minor irregularities in wall outline (Pl. IV, Fig. H), while the extreme condition is found in A. flexuosa of Ecuador (Pl. IV, Fig. K).

The spores of several species were sectioned on a freezing microtome and stained with crystal violet. Even with this coarse treatment there were enough satisfactory sections to show at least the gross aspects of wall construction. The wall is composed of three major layers. The innermost layer, the intine, is very thin and is the most readily stained. The exine, which takes stain only poorly, composes the greater part of the wall, including the ridges, while a thin, clear perine covers the outer surface of the spore.

In the past there have been repeated claims that there is no perine present in the Schizaeaceae (Bower, 1926; Harris, 1955). Recently Bolchovitina (1959) reported a perine in A. lanuginosa and one fossil species, A. mosquensis. This layer, I find, is constant for the subgenus Coptophyllum as well as for Mohria and can most readily be seen in many

species as it falls away from spores mounted in diaphane or acetylized and mounted in glycerine jelly. It has the appearance of a clear cast of the spore, and usually lacks any further ornamentation of its own. In sect. Pachypoda, however, the perine is beset with spicules, 1 to 7 μ high (Pl. IV, Fig. L). Smaller spicules are found occasionally in sect. Anemiaebotrys. These are not readily noticed while the spore is intact, but as the perine falls off, their presence is more evident. The fact that this outer layer does, at times, have some additional ornamentation of its own supports the interpretation that it be considered a perine rather than part of the exine.

In both sect. Coptophyllum and sect. Pachypoda the perine is removed quite readily from the exospore. In such a condition it is difficult to distinguish the ridges on the exospore, which appears nearly smooth. This feature led Chandler (1955) to suggest a relationship between A. gardneri and a fossil, A. poolensis, which was found as smooth spores in Anemia-like sporangia contained within rolled pinna segments. The latter also resembled those of A. gardneri.

On occasional specimens of other species, such as A. villosa and A. tomentosa, the outer surface of the spore is covered with short, hair-like projections. These have been described and illustrated by Bauke (1878) and I have noticed them from time to time. They do not seem to be constant for a species and may have no significance.

As shown by Erdtman (1957) there are three types of structure found in the spore ridges in Anemia and Mohria. These conditions are reflected in the outward appearance of the spores. The first type consists of a solid ridge, showing no internal differentiation whatsoever (Pl. IV, Fig. N). From a surface view these ridges appear clear and homogeneous. Such a condition is the rule in sections Coptophyllum, Pachypoda, and Adetostoma, and the A. villosa group.

A common variation is a granular appearance within the ridge, apparently due to refraction of light on a differentiated portion within the ridge (Pl. IV, Fig. O_2). My sections show that there is a linear medulla running the length of the ridge and containing a fine reticulate or spongy network (Pl. IV, Fig. O_1).

In the third type of ridge there is a medulla, but it appears empty or at least of a different composition from that of the rest of the exine (Pl. IV, Fig. P_1). The external appearance is one of a split ridge on optical sectioning (Pl. IV, Fig. P_2). This medulla may be a small part of the ridge, as in Mohria and occasional spores of A. flexuosa, A. intermedia, and A. elegans. In subg. Anemiorrhiza it composes the greater part of the ridge with the result that the exine covering the medulla is quite thin.

One of the most interesting and yet difficult problems concerning Anemia spores is that of size. Within the subgenus Coptophyllum their size ranges from 45 to 172 μ in diameter. Only in a general way can spore size be used in distinguishing species or species groups. Spore size is often characteristic of a species, but occasionally there is an extremely wide size range within a species or even on a single plant. The significance of the differences in spore size has not been entirely established in Anemia, but certain aspects of its variation have been worked out.

There is some degree of variation within a species which can be

explained as "natural variation," a variation which has no basis in abnormalities in spore production. However, there are some species and species groups which display a distressingly great variation. Within the sect. Coptophyllum, for example, spore diameter ranges from 45 to 107 μ. The extreme variation in this group is correlated to a large extent with the number of spores produced in the individual sporangia. Bower (1926) cites A. (subg. Anemia) phyllitidis as having 128 spores per sporangium, but the species of subg. Coptophyllum show great variation in this character, as they do in spore size. Anemia buniifolia with the smallest spores of the section Coptophyllum produces about 256 or about 128 spores. On the other hand, A. millefolia has the largest spores of that section and produces about 64 or about 32 spores per sporangium. Anemia rutifolia seems to be constant with 128 spores per sporangium. The figures for spore number are inversely related to size as shown in Table 1. In the species listed there, the spore number per sporangium and range of spore size is characteristic of an individual plant.

Table 1. Comparison of number of spores per sporangium with spore size in section Coptophyllum.

Species	Approximate spore number per sporangium	Spore diameter in μ
A. buniifolia	256	45 - 52
A. buniifolia	128	55 - 59
A. rutifolia	128	58 - 62
A. millefolia	64	65 - 72
A. millefolia	32	94 -107

Variability in spore number is found, however, on individual plants of A. tomentosa var. anthriscifolia and the closely related A. tomentosa var. tomentosa, and A. ferruginea. Accordingly there is variation in size: from single fronds I have obtained spores ranging from 84 to 172 μ in diameter.

Although size differences between species are masked as a result of this phenomenon, one can still make out three general categories based on spore size. Uniform spores generally less than 85 μ in diameter are found in a few taxa, such as A. tomentosa var. australis, A. simplicior, and A. elegans. Uniform spores larger than 85 μ in diameter are found in the majority of species of subg. Coptophyllum. In both of these first two groups, spore size is relatively constant for each taxon, and there are no indications of abnormalities, such as abortion or extreme size variation on a single plant. The third category includes those taxa with large spores and irregularities in size and abortion. The probable significance of these three categories will be discussed in the sections on cytology and irregularities of the life cycle.

Gametophyte

The gametophyte of Anemia has been studied by others in some detail, although certain phases of its development are still in question. Shortly after Hofmeister's fundamental work on the alternation of generations (1857), morphologists became greatly interested in the gametophyte generation of ferns. Much of the work on Anemia was done during the last half of the nineteenth century. Kny was the first to report on Anemia gametophytes (1869, A. hirta [perhaps A. phyllitidis in horticulture]). He pointed out the peculiar formation of the thallus by means of a marginal meristem, producing a very lop-sided gametophyte. Other workers followed with more detailed examination of the gametophytes of the genus. I list these workers as follows, giving the identification that they used: Burck, 1875 (A. fraxinifolia, A. longifolia, A. phyllitidis); Bauke, 1876 (A. hirta), and 1878 (A. cheilanthoides, A. collina, A. phyllitidis); Heim, 1896 (A. dregeana, A. fraxinifolia, A. phyllitidis). The only workers in this century to study Anemia in detail have been Twiss, 1910 (A. phyllitidis), and Momose, 1949 (A. phyllitidis), although Stokey (1951) has mentioned certain peculiarities of it (A. phyllitidis, A. mandiocana, A. adiantifolia).

In my studies, spores were obtained for germination both from living plants at the University of Michigan Botanical Gardens and from dried herbarium specimens. Various media were used as substrates (Prantl's nutrient solution, Knop's nutrient solution, distilled water, broken pottery in distilled water or nutrient solution, Knop's nutrient agar, leaf mold). When fresh spores were used, they germinated on the liquid media in three to five days. However, spores sown in leaf mold and nutrient agar took from ten days to two weeks for germination. It was found that in many cases gametophytes would develop to maturity on a liquid medium, but needed to be transferred to leaf mold in order for the young sporophytes to develop better. Another advantage of using a solid medium is that Anemia spores, especially those of subg. Coptophyllum, are so large and heavy that a majority of them will not float on a liquid medium. Germination on broken pottery or on liquid media and subsequent transfer to soil, however, proved satisfactory.

Spores from herbarium specimens required from one to three weeks for germination, depending on the date of collection. Certain fern spores have been found to be viable after many years in a dried state (e.g., 70 years, Grover, personal communication; 34 years, my own work on Pellaea, unpublished). The greatest longevity exhibited in the Anemia specimens studied was fourteen years, although most of them were less than four years old. The reason for the lack of successful germination of spores on most dried specimens is not known for certain, though their age and the particular drying process used may be factors. Heat-drying probably kills the spores.

The most complete studies in the present work were on Anemia tomentosa, but some were also carried out on A. adiantifolia of subg. Coptophyllum, and A. phyllitidis, A. jaliscana, A. hirsuta, and A. underwoodiana of subg. Anemia.

The first visible signs of germination occur when the spore breaks open along the triradiate crest (Pl. V, Fig. A). A rhizoid appears first,

closely followed by the first green cell of the prothallium (Pl. V, Figs. A_2, A_3). The rhizoid is attached directly to this green cell contrary to Twiss' claim (1910) that they are separated by a second green cell. She states that this intermediate cell is not readily seen in the early stages of development and that it becomes evident only later when the filament is well formed. Indeed, in later stages there is often a cell located between the basal cell and the first rhizoid, but usually this is cut off only after a short filament is formed.

The basal cell elongates and divides by a cross wall. This process is continued until a short filament is formed (Pl. V, Figs. A_4, A_5). At that time the first longitudinal divisions take place, but these are nearly always in cells of the filament below the apical cell (Pl. V, Fig. A_6). The latter continues to divide by cross walls while the other cells divide, at first by longitudinal walls and then irregularly. The divisions are soon limited to one side of the thallus, and a marginal meristem takes over the further growth of the prothallium. The result is a lop-sided prothallium with the original apical cell and part of the original filament located at one side (Pl. V, Figs. A_7, D_1, D_2). Occasionally a second wing will form on the opposite side. This wing may be smaller than the first or equal to it (Pl. V, Figs. D_3, D_4, D_5, D_6).

The cells of the wings are straight-walled and often possess peculiar collenchymatous thickenings in the lateral walls (Pl. V, Fig. B), as described first by Bauke (1876) and subsequently by other authors, Heim (1896), Momose (1949) and Stokey (1951). The thickenings are located at the corners of the cell and apparently randomly along the wall. Lygodium and Mohria share this character with Anemia. Outside the Schizaeaceae these thickenings are recorded only in Adiantum and Cheilanthes (Bower, 1928).

Distinctive unicellular trichomes are found along the margin of the prothallium and less commonly on the upper and lower surfaces (Pl. V, Fig. C). They are more or less reniform, attached terminally, and appear nearly colorless. The long axes of the majority of them are pointed toward the apex of the original filament. Heim (1896) reports that they contain tannic acid, but no actual biochemical tests are mentioned.

Most of the rhizoids are formed along the side of the prothallium occupied by the original filament, and it is here that the thickened cushion is formed. Antheridia are found alone on the gametophyte or mixed with archegonia. They are borne on the cushion and on the wings of the prothallium, in some cases on the dorsal surface as well as the ventral. Male prothallia seem to be more irregular, as a rule, frequently having a lateral branch or lobe, Burck's (1875) "pousse latérale normale." As Bauke (1878) points out, these are not special branches but merely part of the irregular male prothallium.

The development of the antheridium is illustrated in Pl. VI, Figs. A_1, A_2, A_3. A cell of the prothallium divides periclinally, and the outer cell divides again to cut off a thin basal cell. Occasionally this basal cell redivides to form a short stalk. The outermost cell then cuts off what will become the ring cell and redivides to form a cap cell and a central cell. The latter, as Davie (1951) points out, swells, forcing its way down into the subtending cells, which then become ring-shaped. The cap

cell will rarely divide again to make a cap on itself like that of Lygodium.

The number of sperms produced in the antheridium of A. phyllitidis is reported to be 156 (Twiss, 1910), a high number in keeping with the relative primitiveness of the genus. Optical sectioning of the antheridium of A. adiantifolia has shown that this, too, has a high number of sperms (30-50 in one optical section). Lygodium has 128 sperms. However, A. tomentosa vars. anthriscifolia and mexicana produce a relatively low number of sperms (25-30). As will be discussed later, subg. Coptophyllum (including A. tomentosa) is the most primitive of the genus. Though it is supposed that a high number of sperms is a more primitive condition than a low number and hence would be expected to be present in subg. Coptophyllum, apparently a reduction in sperm number has occurred in at least part of this subgenus since the evolutionary separation of the subgenera.

There has been some disagreement regarding the method of sperm release. Burck (1875) and Heim (1896) claim that it is by a star-shaped crack in the cap of the antheridium whereas Bauke (1878) reports that the entire cap falls off. In all the cases I have seen, the entire cap is released (Pl. VI, Fig. A_4, A_5). Other interpretations may be due to the star-shaped cavity which forms within the antheridium after the sperms have been released.

The archegonia are borne on the ventral surface of the gametophytic cushion. Gametophytes bearing archegonia tend to be more regular in shape than those bearing only antheridia and often form two nearly equal wings. Twiss (1910) reports that archegonial development is similar to that of Lygodium and the Polypodiaceae. The neck consists of four rows of cells with four to six cells in each (Pl. VI, Fig. B). Here again there is a contrast with A. phyllitidis (Momose, 1949) and A. adiantifolia, each of which has five to nine cells in the archegonial neck. The neck is strongly curved toward the apex of the cushion, a condition peculiar to Anemia and opposite that seen in most higher ferns that have been reported.

There is considerable variation of gametophytic form within the Schizaeaceae. In Schizaea the gametophytes are strictly filamentous, much like those of Trichomanes. In Lygodium, as in Anemia and Mohria, the gametophyte grows by a lateral meristem, but it is usually cordate in form. There are no papillae and the archegonial necks are directed vertically or toward the base of the cushion, rather than toward the apex as in Anemia.

Although Bauke (1878) and Heim (1896) report on the gametophytes of Mohria, the recent study by Atkinson (1961) is the most complete. As in so many other characters, Mohria displays a very close similarity to Anemia in the gametophyte. Growth is by a lateral meristem and forms a lop-sided thallus. On the basis of gametophytic studies, Momose (1949) supports Nakai's recommendation (1937) that the family be broken into three families, Mohria being placed with Anemia in the Anemiaceae and the other two genera alone in their own families of Lygodiaceae and Schizaeaceae.

Although lop-sided growth of the gametophyte is notable in Anemia

and Mohria, it occurs in certain members of the cheilanthoid ferns as well, such as Actiniopteris, Onychium, and Acrostichum (Stokey, 1951). Other characters common to these two groups will be discussed later.

Spore Abortion and Abnormalities of the Life Cycle

As mentioned earlier, there is extreme variation in spore size in several species of subg. Coptophyllum and most notably in Anemia tomentosa. Another unusual feature in this species is that of widespread spore abortion—not complete abortion in a few plants but a small percentage of abortion in many plants. I have studied two living plants of this species at the University of Michigan Botanical Gardens, viz. one of A. tomentosa var. australis and one of A. tomentosa var. anthriscifolia, both from Argentina. In most outward appearances they are similar, but their spores show remarkable differences.

The plant of A. tomentosa var. australis, collected by E.R. de la Sota in Tucumán, has spores fairly uniformly about 80 μ in diameter, and appearing normal in every way. The other plant, A. tomentosa var. anthriscifolia, was collected by J. Lichtenstein in Córdoba, Argentina. Its spores are highly variable in size, ranging from 84 to 172 μ in diameter. Most of these spores appear more or less normal, but larger than those of the de la Sota plant, the corners rounder, the protuberances not as distinct, and the ridges more irregular, frequently anastomosing (Pl. IV, Fig. M). The largest of these spores, moreover, are giant spheres, accompanied by many abortive spores and miscellaneous particles.

The spore number per sporangium also differs in the two plants. The de la Sota plant regularly has 64 spores, or nearly so, per sporangium. The Lichtenstein plant, on the other hand, has a highly variable number, related inversely to the size of the spores found within; the smaller the number of spores, the larger their size. The numbers of spores found in sporangia do not fall into a regular pattern or sequence of a factor of 2, as 128, 64, 32, as one might expect, but various intermediates are also found as shown in Table 2.

Herbarium specimens of A. tomentosa from South America can be placed in the two classes represented by these plants, i.e., those with a constant number of spores per sporangium, uniform spore size, and little or no abortion, as opposed to those with a variable number of spores per sporangium, variable spore size, and frequent abortion.

Spores from these two plants were sown under uniform conditions and the resulting gametophytes display further differences. Those that arise from spores of the de la Sota plant appear normal, with typically lop-sided to subcordate prothallia and producing antheridia and archegonia. Reproduction is apparently sexual, although no sporophytes were produced in my cultures.

The Lichenstein gametophytes, on the other hand, are more irregular in shape, many of them attenuate or nearly filamentous, few attaining a cordate or even a normal, lop-sided form (Pl. V, Fig. E). Although many antheridia are produced on some prothallia, sporophyte production is asexual by apogamy. Both the gametophyte and sporophyte generations have the triploid chromosome number, as will be discussed below. A small area thickens near the margin on either the dorsal or ventral

Table 2. Spore number and average diameter from selected sporangia of two plants of A. tomentosa.

de la Sota plant		Lichtenstein plant	
Spore diameter in microns	No. of spores per sporangium	Spore diameter in microns	No. of spores per sporangium
83	61	95	118
85	56	101	88
74	52	106	48
86	52	135	28

surface of the gametophyte. Occasionally this thickening is found on the most filamentous prothallia. A few multicellular hairs appear on this area, and soon the swelling develops into a small bud. The first few leaves are more or less fan-shaped and look like those of sexually produced sporophytes. There is no foot produced into the gametophyte tissue, and roots are very slow in developing. Although the first root may form as soon as the second or third leaf, it often does not appear until after the fifth leaf is produced. Tracheids are frequently found in the gametophytes, a common condition in apogamy.

Only rarely are archegonia produced on these gametophytes. When they do appear, it is only after the initiation of the apogamous buds. No sexually produced sporophytes were seen, but this does not exclude the possibility of occasional sexual reproduction. The abundance of archegonial production in other apogamous ferns has not been reported. Although Steil (1939) says archegonia may be produced on apogamous prothallia, Manton (1950) claims apogamous gametophytes are devoid of archegonia. The mere presence of them on Anemia gametophytes suggests the possibility of two possible types of reproduction on the same gametophyte. Perhaps under certain conditions sexual fusion might be achieved.

Meiosis apparently does take place in the sporangia of these apogamous plants. Normal meiotic figures were observed in each case, and the resulting spores were all in tetrads. Chromosome squashes of meiotic sporangia of the Lichtenstein plant show a count of n = 114. Thus, the spore mother cells must be hexaploid. After meiosis the resulting spores and gametophytes are necessarily triploid. Since there is no sexual fusion, the apogamously produced sporophyte plant must also be triploid. Somatic squashes of root tips from the parent plant reveal n = 114, as expected. Therefore, the chromosome number must double within the sporangium prior to meiosis to produce hexaploid spore mother cells. According to Manton (1950) this is the usual procedure in apogamous ferns.

Similar apogamous reproduction was also found in my cultures of A. ferruginea var. ferruginea. On the basis of close similarities in spore morphology and in irregularities, I presume that this type of reproduction is the rule also in A. ferruginea var. ahenobarba and A. tomentosa var. tomentosa. Gametophytes of A. tomentosa var. mexicana, however,

were strictly sexual in my cultures, like var. australis. All other species cultured appear to have normal, sexual gametophytes with the possible exception of A. (subg. Anemia) jaliscana. Previous workers make no mention of the apogamous mode of reproduction in Anemia. The species on which they worked all have normal spore production and are presumably sexual. The one possible exception is A. cheilanthoides [= A. tomentosa var. tomentosa]. Bauke (1878) studied this species but makes no mention of it beyond the thallus stage. If it were really A. cheilanthoides, and it grew to maturity, he should have found the apogamous buds, which are readily formed. I conclude that either the plant was misidentified or his gametophytes died before reaching maturity.

CYTOLOGY

Prior to this study, chromosome counts had been obtained for only two species of Anemia, A. phyllitidis (n = 76) and A. rotundifolia (n = 38) by Manton and Sledge (1954). Both of these belong to subg. Anemia. Data from my own counts are shown in Table 3.

In spite of the few counts made in the genus, there is enough evidence to postulate the probable ploidal levels of some of the other species. It is often possible to correlate chromosome number with spore size and by extrapolation to determine the probable chromosome number of dried specimens, as was done extensively in the fern genus Cystopteris, for example, by Blasdell (1959). Spore diameter and stomatal length were compared in those taxa of subg. Coptophyllum for which the chromosome number is known. These data appear in Table 4.

Because spore size in Anemia may vary greatly on individual plants, between species, and with spore number per sporangium, the precise genomic situation is difficult to assess. The diploid A. tomentosa var. australis has by far the smallest spores, but the other two varieties of A. tomentosa have widely different spore sizes in spite of the fact that their spores have the same chromosome number. The greater size of A. tomentosa var. anthriscifolia, however, may be related to its irregularities in spore production. Furthermore, the tetraploid A. karwinskyana has larger spores than the hexaploid A. tomentosa var. mexicana.

Stomatal size in these four taxa increases with the chromosome number of the sporophyte plant. Although there seems to be a direct correlation of stomate size with chromosome number, the similarity in size of the polyploids makes stomatal length impractical as a diagnostic indicator of precise chromosome number. It is clear, then, that although the size of spores and stomates is related to chromosome number, it is not possible to judge accurately the precise genomic level on this basis alone. This may be feasible in some cases among closely related species, but comparison of more distantly related species, such as A. tomentosa and A. karwinskyana is not as meaningful.

One feature that stands out clearly, however, is the discernible gap in these measurements between diploid and polyploid species. This break is substantiated by examination of the other species of subg. Coptophyllum. It appears that a stomatal length of 40 μ and a spore diameter of 85 μ usually divides the diploid from the polyploid condition. Although

Table 3. Chromosome observations.

Species	Meiotic counts, except as noted
COPTOPHYLLUM	
A. karwinskyana (Presl) Prantl	
MEXICO: Gro., 2.9 mi. n. of Nueva Ixtapan, Mickel 710.	76
A. tomentosa var. australis Mickel	
ARGENTINA: Cerca de Tucumán, de la Sota s.n.	somatic, ca. 76
A. tomentosa var. anthriscifolia (Schrad.) Mickel	
a. ARGENTINA: Villa General Belgram, Sierra Chica, Lichtenstein s.n. (apogamous) (Pl. VI, Fig. E).	somatic, 114
b. BRAZIL: Rio Grande do Sul, São Leopoldo, Sehnem s.n.	114
A. tomentosa var. mexicana (Presl) Mickel	
MEXICO: Oaxaca, Cerro San Felipe, Mickel 760.	114
ANEMIA	
A. hirsuta (L.) Sw.	
a. MEXICO: Colima, rd. from Manzanillo to Durazno, Mickel s.n.	76
b. MEXICO: Gro., 2.9 mi. n. of Nueva Ixtapan, Mickel 711.	76
c. JAMAICA: Proctor s.n.	76
A. cf. oblongifolia (Cav.) Sw.	
MEXICO: Gro., 2.9 mi. n. of Nueva Ixtapan, Mickel 712.	114
A. phyllitidis (L.) Sw.	
Cultivated at Harvard Bot. Gard.	76
A. underwoodiana Maxon	
a. DOMINICAN REPUBLIC: Jimenez s.n.	76
b. JAMAICA: Proctor s.n.	76
ANEMIORRHIZA	
A. adiantifolia (L.) Sw.	
a. JAMAICA: Proctor s.n. (Pl. VI, Fig. E_1).	38
b. MEXICO: SLP, 28.8 mi. e. of Ciudad de Maíz, Mickel 571.	38
c. MEXICO: SLP, 3 mi. n. of Tamazunchale, Mickel 616.	38
A. mexicana Kl.	
a. MEXICO: SLP, 3 mi. n. of Tamazunchale, Mickel 617.	38
b. MEXICO: SLP, 3 mi. s. of Tamazunchale, Mickel 619.	38
A. adiantifolia (L.) Sw. X mexicana Kl.	
MEXICO: SLP, 3 mi. n. of Tamazunchale, Mickel 618.	38 (irregular pairing)

Table 4. Comparison of spore and stomatal size with chromosome number.

Taxon	Somatic chromosome number	Approx. stomate length (μ)	Approx. spore diam. (μ)
A. tomentosa var. australis (sexual)	2x = 76	37 (32-45)	81 (68-81)
A. tomentosa var. anthriscifolia (apogamous)	3x = 114	43 (32-49)	104 (84-172)
A. tomentosa var. mexicana (sexual)	6x = 228	47 (42-55)	91 (75-110)
A. karwinskyana (sexual)	4x = 152	46 (42-55)	98 (75-107)

spore size may vary between species and species groups, stomatal length seems to be more conservative and often can be used when spore size does not clearly indicate the ploidal level. Using these data, we can postulate the ploidal level of other species. For example, A. simplicior (spores ca. 75 μ in diameter and stomates ca. 38 μ long) is probably a diploid. A. ferruginea, on the other hand, has spores ca. 100 μ in diameter and stomates ca. 50 μ long and is probably a polyploid. The precise ploidal level, as explained above, cannot be determined without further cytological information about other key species.

More data are needed to distinguish polyploidy within individual species. Specimens of A. villosa from Venezuela and Colombia are probably polyploids (spores ca. 95 μ, stomates ca. 50 μ). Many of the plants from southern Brazil show markedly larger spores (ca. 104 μ) and stomates (ca. 56 μ). The northern South American plants and some of those from Brazil may well be tetraploids whereas the Brazilian plants with greater measurements could have a higher polyploid level. Differences in polyploid level would help to explain abortion in occasional Brazilian plants. A tetraploid interbreeding with a hexaploid, for example, would almost surely result in sterile pentaploids.

Another anatomical reflection of genomic level is the length of the small, terminally attached unicellular hairs. Their length is nearly equal to that of the stomates, e.g., A. simplicior (33-42 μ), A. tomentosa var. australis (33-45 μ), A. tomentosa var. anthriscifolia (42-55 μ), A. tomentosa var. mexicana (39-52 μ), A. karwinskyana (43-61 μ), and A. ferruginea (39-55 μ) (cf. Table 4). The dividing point of hair length between diploid and polyploid species is not known, but appears to be about 43 μ.

In subg. Coptophyllum, only eight of the forty-two species and varieties are presumed diploids. These few taxa are widely scattered geographically, and most are rare. They are: A. elegans, A. eximia,

A. perrieriana, A. tomentosa var. australis, A. brandegeea, A. intermedia, A. schimperiana, and A. aethiopica.

Some species of the section Coptophyllum show contradictory evidence between the stomates and spores. Although they have small spores (see Table 1), their stomates are quite large (45-72 μ). At least part of their smaller spore size is due to the greater spore number per sporangium (A. buniifolia and A. rutifolia). These species are probably polyploids. On the other hand, A. smithii has large spores (ca. 90 μ) and small stomates (ca. 36 μ). It may well be a diploid as are presumably the closely related A. brandegeea and A. intermedia, which have both small spores and small stomates.

Most species of subgenus Anemiorrhiza are presumed to be diploid. However, subg. Anemia resembles subg. Coptophyllum in that most of its species are polyploid. The one reported diploid, A. rotundifolia, belongs to a group of species—A. rotundifolia, A. herzogii, A. mandiocana, and A. radicans—which have the smallest spores and stomates in the subgenus.

The basic chromosome number for the genus, n = 38, differs from that of other genera of the Schizaeaceae. Lygodium has a basic number of n = 29, 30, and in this respect resembles the cheilanthoid ferns, which the Schizaeaceae resemble in other features as well. On the other hand, the only reported count for Schizaea is n = 77 (Lovis, 1958), which is close to the tetraploid number of n = 76 in Anemia. The chromosome number of Mohria is not known, though from its close relationship with subg. Coptophyllum, I would suspect it to have a base number of n = 38. Tentative observations suggest M. caffrorum to be a diploid (spores ca. 72 μ, stomates ca. 37 μ) and M. lepigera a polyploid (spores ca. 85 μ, stomates ca. 50 μ).

A variety of chromosome numbers have been reported for the genus Ceratopteris: n = 40, 76-78, 77, 78, 120-130, as summarized by Javalgekar (1960). Most of these are very close to the numbers known for Anemia. Ceratopteris has been placed with the cheilanthoid ferns by Bower (1926) and Christensen (1938), but its phyletic affinities are obscure. Further suggestions of its schizaeaceous affinity will be discussed later.

ECOLOGY AND HYBRIDIZATION

Although habitat data are typically scanty on most herbarium sheets, a reliable picture of the habitat has been obtained from a composite of herbarium data, floristic works, and personal observations. For most species of subg. Coptophyllum, the habitat is strikingly similar; they usually occur on well-drained slopes at an elevation of 300-2300 meters. The actual elevation depends in part on latitude. For example, in Mexico and Argentina they are usually found from 300-2000 meters, whereas in Peru and Ecuador they seem to be most common at 1000-2300 meters.

The soil is sandy, rocky, clay or loam which is slightly less than neutral. A. tomentosa var. australis is found in soil with a pH of 5.8. Frequently Anemias are associated with rocks (e.g., "rocky slope," "under rocks," "among rocks," "upon a humid rock"), such as granite, quartzite, sandstone, or schist.

They are usually found in the open or in partial shade (e.g., "prairie," "pine-oak forest"). Legrand (1958) says of A. tomentosa var. tomentosa in Uruguay, "Podemos considerarla algo heliófila."

Not all species follow this pattern. Anemia myriophylla is found at higher altitudes (2000-3200 meters), whereas the species of Uruguay, Paraguay, northeastern Argentina and southernmost Brazil are found at much lower elevations, such as 35 meters, 70 meters, and 200 meters.

Probably not all species occupy the same habitat, but there is certainly considerable overlap in their ecological preferences. Quite frequently several species are found growing in the same association, a situation referred to by Wherry (1961) as a genus community. I have seen as many as four species of Anemia growing together in Mexico. Their gregariousness is further evidenced by the great frequency of mixed collections.

These mixed collections include not only distantly related species, but also closely related species, and various hybrids. In some cases the coexisting species are extremely difficult to distinguish morphologically, and seem to grade into one another, but intermediate specimens are shown to be sterile. For example, I have seen three sheets of Damazio 1381: one is A. imbricata, as labelled; one is the closely related A. villosa; and the third is a sterile intermediate. Thus affinity tests by hybridization have been worked out naturally in the field, and groups of specimens, including the parents and the hybrids of these natural experiments, have been collected in toto inadvertently by unsuspecting botanists.

The sympatric nature of very closely related species presents the question of whether these species arose sympatrically or whether they differentiated in isolated areas and have since been brought together. The latter would seem to be the more probable condition. Sympatric speciation would necessarily involve a breeding barrier between the two derived species in order for them to differentiate. Otherwise, introgression would wipe out their identities.

Previous to this study there were only five reported hybrids within the genus Anemia. Prantl (1881) cited three, and Brade (1948) another, all involving members of the subgenus Anemia. In 1905 Rosenstock made a binomial, A. ulbrichtii, for a hybrid between A. (subg. Anemia) phyllitidis and A. (subg. Coptophyllum) flexuosa. This is the only known case of intersubgeneric hybridization in Anemia. It is particularly noteworthy considering the age of the genus; these two subgenera have probably been diverging since the Oligocene, and there is a great phyletic gap between the two putative parents.

In my studies I have found six additional and heretofore undescribed hybrids within subg. Anemia, seven in subg. Coptophyllum, and one in subg. Anemiorrhiza. These plus the five previously described make a total of nineteen now known in the genus. All but two of these—A. X ulbrichtii and A. X jaliscana—are known from less than ten specimens. Within subg. Coptophyllum, A. villosa is the most promiscuous. It has apparently formed crosses with four other species; A. raddiana has crossed with three. None of the rare species is found to hybridize, even though they sometimes occur in the same populations with other species.

Frequent hybridization in Anemia is probably due in part to the tendency of the species of Anemia to grow together in the same habitats.

Whereas in most genera closely related species tend to be isolated geographically or ecologically, in Anemia even the most closely related species may be found living side-by-side in the same populations. This phenomenon is not merely occasional but almost the rule.

FOSSIL HISTORY AND MODERN DISTRIBUTION

The genus Anemia is unusual in being one of the few modern genera of ferns with a fairly ample fossil history. Even more exceptional is the fact that its presumed immediate ancestor, Senftenbergia, places the beginnings of this group back as far as the Lower Carboniferous. The time of origin of Anemia is not known for certain, but is thought to have been in the late Jurassic.

The unifying character of the Schizaeaceae is the distinctive sporangium with its annulus consisting of a subapical ring of thickened cells. The earliest plant with such a structure is Senftenbergia. Its schizaeaceous affinities were noticed by its discoverer, Corda, in 1845, but detailed studies of the sporangium were not made and its relationship not definitely established until its detailed structure was revealed by Radforth (1938, 1939). He found that the sporangium closely resembled that of Anemia in most respects, differing chiefly in having a short basal stalk and an annulus composed of a multiseriate row of bow cells. An annulus of more than one cell width is found today only in some species of Lygodium, such as L. lanceolatum (Bower, 1926). The apical plate in Senftenbergia is composed of several cells, as in Anemia, whereas those of Lygodium and Schizaea usually have only one. The sporangium of Lygodium is also distinct in being attached laterally and held nearly at right angles to the lamina. The sporangium of Schizaea more closely resembles that of Anemia and Senftenbergia but is more slender. Of the extant genera of Schizaeaceae, Senftenbergia most closely resembles Anemia. Its spores and lamina, however, are quite different.

Radforth observed trends of sporangial specialization among the three species of Senftenbergia found in Carboniferous deposits, including reduction in the basal stalk and in the number of rows of cells in the annulus from five to only two. In the Jurassic, there appeared the genera Norimbergia and Klukia, which had single-rowed annuli, as in most modern Schizaeaceae.

Several other schizaeaceous genera with spores much like those of Anemia have been described from the Lower Cretaceous: Schizaeopsis, Schizaeopteris, Ruffordia, and Pelletieria. All of these, however, have fronds quite distinct from those of Anemia. Reed (1948) gives a good summary of these fossils.

Fossils referred to Anemia itself occur both as megafossils and microfossils. The megafossils consist mostly of sterile frond impressions whose venation has been compared with that of Anemia. In view of the repetition of foliage types in ferns and fern-like plants, this would seem to be tenuous evidence for placing a fossil in a modern genus, but Andrews' discovery of a fertile frond of A. fremontii (Andrews and Pearsall, 1951) dispels some of the doubt. Its fertile pinnae were held erect in the typical fashion of modern species. Frond impressions of

Anemia have been reported from western and southern United States, England, and Siberia.

Many fossil spores have been found which bear a close resemblance to those of modern Anemia species, in particular those of subg. Coptophyllum. In most cases these have been referred to form genera, such as Cicatricosisporites, Appendicisporites, Corrugatisporites, and Striatriletes, but occasionally to the modern genera Anemia and Mohria (Chandler, 1955; Bolchovitina, 1953, 1956, 1959). Striate spores have been found in North America, western Europe, Siberia, Australia, and Colombia. Most were smaller than those of subg. Coptophyllum today, ranging from 25 to 60 μ in diameter. This does not necessarily imply a lower chromosome number. Anemia (subg. Anemia) rotundifolia, known to be a diploid (n = 38), has spores as small as 35 μ in diameter. As explained above, the number of spores produced per sporangium greatly influences spore size.

Whether all of these fossil spores are actually Anemia is not known. Since other genera of the Cretaceous are known to have striate spores, it is possible that these spores may belong to these genera or to undescribed genera of the group. Apparently during the late Jurassic and Cretaceous there existed a complex of closely allied schizaeaceous genera from which Anemia and Mohria arose. Assuming that these megafossils and microfossils belong to Anemia or its close relatives, Anemia probably arose in the late Jurassic and reached its peak of development in the Cretaceous. At that time it lived throughout most of the world.

Apparently there was considerable speciation if we can judge by diversity in the fossil spores. Bolchovitina (1959) estimates there are forty fossil species of Anemia, and twenty of Mohria which she has since combined with those of Anemia under Pelletieria (personal communication). L.R. Wilson has found eighteen fossil species of Anemia spores from the United States (personal communication).

The latest Anemia spores in Australia are found in Upper Cretaceous deposits, and the latest records of Anemia in Europe, Asia, and North America are from the Oligocene. A general cooling of the higher latitudes in the late Oligocene was probably the cause of the disappearance of the genus in those areas, limiting it into the tropical areas where it is today. The most recent record of fossil Anemia is from the Miocene of Colombia (van der Hammen, 1957). It is quite possible that more recent fossils of Anemia lie undiscovered in tropical parts of the world.

Subgenus Anemia is found throughout Latin America and one species occurs in South Africa. Subgenus Anemiorrhiza is limited to the calcareous soils of the Caribbean region. The present-day range of subg. Coptophyllum covers nearly the entire distribution of the genus. In general this includes the upland areas of tropical and subtropical America, Africa and southern India. In spite of the broad range of the subgenus, only a few of the thirty-eight species are common over a large area. Most of the species are endemic to small areas or are rare. Twenty-three of the species are known to me by fewer than ten specimens. Geographical range is narrow enough in many species to be of value for identification purposes. There are no species which are found both in the New and Old Worlds, but several Old World species have close relationships with species of the Americas, such as A. perrieriana with A. aspera, and A. lanipes with A. lanuginosa and A. gardneri.

The nine species of subg. Coptophyllum in Africa apparently cover most of the upland area of the continent from Ethiopia in the east to the Union of South Africa in the south and French Guinea in the west. For the most part they seem to be rare and have been poorly collected. Each of the species seems to be limited geographically with little overlap of range with the others (Pl. VII, Fig. B). There is one species in southern India.

The subgenus has two centers of endemism in America. Of the twenty-eight New World species, twenty are found in Brazil, and eleven of these are endemic to that country. Six species are endemic to Mexico and Central America. These areas probably contain representatives of the ancient Anemia flora while the North American representatives were either eliminated or forced into Central or South America by the cooler climates of the Oligocene and the subsequent Pleistocene glaciation. On the contrary, it is possible that a new spurt of evolutionary activity is taking place in the present areas of endemism, although this seems less probable.

Because the primitive elements are in both Madagascar and Brazil, one might suppose, judging solely from the present distribution of the subgenus, that this supports Copeland's view (1939) of the Antarctic origin of the ferns. Assuming an origin in the southern hemisphere, the Gondwanaland or Continental Drift theories might also be used to explain the present distribution. However, application of fossil evidence reveals that modern distribution may be construed merely as a remnant of past world-wide distribution, and its place of origin is more indefinite.

Aside from the species restricted to Brazil, four types of broad distributional patterns of American species and species groups can be pointed out.

Species of sect. Adetostoma are found in the mountains from Bolivia to Central America and Mexico (Pl. IX, Fig. B); A. flexuosa occurs only in the Andes (Pl. IX, Fig. D).

A second type of range includes those species found both in northern South America and southeastern Brazil which are connected in distribution, not along the Andes but along an easterly route around the Amazon Basin. Anemia villosa and the species of sect. Coptophyllum follow this pattern (Pl. VIII, Figs. A, B). Because of a paucity of records from the central Brazilian highlands and northeastern Brazil, some of these species appear disjunct.

The A. simplicior group includes A. simplicior and A. raddiana in southern Brazil and Paraguay and A. bartlettii in British Honduras (Pl. IX, Figs. A, D). Such a disjunct distribution is also found in A. (subg. Anemia) hirta.

Finally, the A. karwinskyana group of species is limited entirely, so far as we know, to Mexico and Central America (Pl. IX, Fig. A).

FAMILIAL AND GENERIC RELATIONSHIPS

The Schizaeaceae is undoubtedly an isolated family, and relationships with other modern families are tenuous. Though family relationships are obscure, as might be expected from its great age, its probable nearest affinities lie with the cheilanthoid ferns (Gymnogrammaceae). Anemia and Mohria especially have many features in common with this group. Both families are epipetric and terrestrial; both have tetrahedral spores, and spore size is highly variable within individual species. Harris (1955) reports high standard deviations in spore size from Schizaea (s = 7 μ), Lygodium (s = 10 μ), and Cheilanthes (s = 8 μ), whereas in most ferns the standard deviation is 2-4 μ. The vascular bundle of the stipe in both groups is nearly the same. Neither Anemia nor the cheilanthoid ferns has the usual circinate vernation; both have, rather, a nodding habit during early frond development (Pl. XXVII, Fig. A). The peculiar lopsided gametophytes of the Schizaeaceae are found again in certain genera of the Gymnogrammaceae; and the unusual collenchymatous gametophytic thickenings are found also in Adiantum and Cheilanthes. The chromosome number of the Gymnogrammaceae is typically n = 29 or n = 30, which agrees with that of Lygodium.

Although none of these characters is significant by itself, the accumulation of so many features in common strongly suggests their affinity. Occupying perhaps an intermediate position phylogenetically between the two families is the genus Negripteris. Pichi-Sermolli (1946) places it in his Schizaeales as a separate family. Its range is in eastern Africa, as is that of Mohria and some species of Anemia. Its sporangium is peculiar in having a very broad annulus, distinct from that of other cheilanthoid ferns, but only vaguely like that of Anemia. Each sorus has only one to five sporangia, suggesting transition from the schizaeaceous monangium to the plurisporangiate sorus of the higher ferns. Its petiole trace resembles that of Anemia and the Gymnogrammaceae. Finally, spores of Negripteris are slightly reminiscent of those of Anemia aethiopica in their anastomosing series of ridges.

One further possible relationship of the Schizaeaceae is to the genus Ceratopteris. Both the distinct morphology of the sporophyte of Ceratopteris and its aquatic habitat have caused botanists to place it by itself in the family Parkeriaceae. As mentioned above in connection with cytology, relationships between Ceratopteris and the cheilanthoid ferns have been proposed; but Ceratopteris also bears a definite similarity to Anemia in certain respects. Its chromosome number (x = ca. 40) is much closer to that of Anemia (x = 38) than to that of the Gymnogrammaceae (x = 29, 30). Its spores are the only ones among those of modern ferns which resemble those of Anemia. Fossil spores of this genus were reported with those of Anemia by Bolchovitina (1953), so it could well have been derived at an early time from Anemia-like ancestors. Ceratopteris resembles Negripteris in its broad annulus. Other characters of the sporophyte are difficult to compare, however, owing to adaptations to the aquatic habitat.

Relationships among the genera of the Schizaeaceae are equally obscure. Although the present research has dealt chiefly with species of Anemia, a few general features of the phylogeny within the family may

be pointed out. All four genera show a combination of primitive and advanced characters. Bower (1926) cites Anemia and Mohria as the most advanced stelar type, but Lygodium and Schizaea are also specialized in many respects. They are both bizarre in leaf habit: Lygodium is a climbing fern, and Schizaea a long-petioled, slender, grass-like fern, whereas Anemia and Mohria have the more usual pinnate architecture.

Lygodium is further advanced in having its sporangium attached laterally. Although Schizaea shows similarities to Anemia in its sporangium, chromosome number, and in the striate spore walls of certain species, it is unique in its bilateral spores and filamentous gametophytes.

The close relationship between Anemia and Mohria has proven useful in establishing the primitive characters for Anemia. Many characters in common between Mohria and subg. Coptophyllum are thought to have been present in the common ancestor and consequently are the primitive ones for Anemia. The two genera probably had a common ancestor. They diverged in several characters which are considered important taxonomically, the more advanced subgenera of Anemia keeping these characters but diverging more rapidly in many peripheral characters. The genus Anemia is unified by (1) localization of the sporangia on the basal pinnae, (2) having oval rather than spherical sporangia, and (3) having hairs instead of scales.

I have treated Anemia, Anemiorrhiza, and Coptophyllum as subgenera rather than genera as Reed (1948) has done. The close relationship of the three is suggested by intermediate morphology in some groups and by the intersubgeneric hybrid, A. X ulbrichtii. Although I disagree with Reed's treatment, I can appreciate the incentive for raising the taxa to higher ranks. When any group of plants is studied in great detail, further differences will emerge that had been previously overlooked. As these differences are correlated, they must be categorized to illustrate their relationships. Thus, closely related species are grouped into sections, the existing sections made into subgenera, and the subgenera made into genera. However, if there is to be any semblance of stability in the generic concept, we must not yield to these pressures at the generic level without a careful evaluation of the evidence. Rather, the use of infrageneric categories is recommended.

The characters and relationships of Mohria and the three subgenera of Anemia are summarized diagrammatically in Plate X. This was constructed on the basis of the "common ground plan" method developed by Dr. W.H. Wagner, Jr., in his taxonomy courses at The University of Michigan and used by various authors, including Hardin (1957), Iltis (1959), and Stern (1961).

A list of characters showing evolutionary trends is compiled. Whether a particular character-state is primitive or specialized is determined on the basis that features common to most or all of a number of related taxa are probably undifferentiated from those of their common ancestor. On this basis, character-states occurring in all or most species of Anemia are probably the primitive ones. For example, smooth spore ridges are found in two of the three subgenera of Anemia and in the closely related genus Mohria, whereas spiny ridges occur only in subg. Anemia. Smooth spore ridges, therefore, are considered to be probably more primitive or generalized than the spiny ones.

Whenever meaningful comparisons can be made, it is important also to compare characters within the whole family Schizaeaceae and in the Filicineae at large. Comparison within Anemia alone, for example, would suggest that upright fertile pinnae are primitive, whereas comparison with other fern groups indicates that this is probably not the case; the few species of Anemia with horizontal fertile pinnae are in this respect most like the generalized ferns as a whole. We must conclude, then, that although the less differentiated species are in the minority in the genus Anemia, the upright fertile pinna condition is specialized.

Each taxon is then compared with the list of characters and given a value of 0 if the character has the generalized state in that taxon or a value of 1 if the state is specialized. These numbers are then totaled for each species, the result being its specialization index, or value. Thus, a taxon with a specialization value of 2, such as Mohria, is not considered as specialized phylogenetically as the genus Anemia subg. Anemia with a value of 8. Relationships are based on correlation of common characters. The evidence in support of the evolutionary evaluation of characters is described below.

A. RHIZOME HABIT. The compact rhizome with caespitose leaves is the rule for both Anemia and Mohria, whereas the creeping habit is found only in Anemia subg. Anemiorrhiza.

B. AXILLARY POCKETS. Invaginations of the leaf axils form deep pockets in the rhizome in subgenera Coptophyllum and Anemia. The absence of such pickets in subg. Anemiorrhiza and the other genera of the family suggests that their presence is a derived condition.

C. RHIZOME INDUMENT. In Anemia, Lygodium, and Schizaea, the rhizomes are clothed with filamentous hairs. Although branched hairs are reported for some species of Lygodium, true paleae or scales are found only in the genus Mohria.

D. PHYLLOTAXIS. The leaves are arranged in a polystichous fashion in all genera and subgenera of the Schizaeaceae except Anemia subg. Anemiorrhiza. The distichous condition of the latter may be correlated with its creeping habit.

E. FROND DISSECTION. In both Mohria and subg. Coptophyllum the usual dissection is bipinnate to bipinnate-pinnatifid. Fronds only once pinnate are found in a large part of subg. Anemiorrhiza and in nearly all members of subg. Anemia.

F. STOMATAL POSITION. In nearly all groups of ferns, the stomate is located on the distal wall of a subsidiary cell. Such is also the case in Mohria and subg. Coptophyllum, but the floating stomate is found throughout subg. Anemia and independently in subg. Anemiorrhiza and in two sections of subg. Coptophyllum.

G. GLANDULAR HAIRS. The multicellular hairs of the lamina have a glandular tip cell in Mohria, and the subgenera Coptophyllum and Anemia. Only Anemiorrhiza has a pointed, nonglandular hair tip.

H-K. FERTILE PINNAE. The "fertile spikes" of Anemia are construed as modified vegetative pinnae, and therefore any deviation can be considered as a specialization. Localization of sporangia on the lowermost pair of pinnae in Anemia (H) is probably derived from a frond bearing sporangia on normal pinnae. (Extreme frond dimorphism has apparently occurred secondarily in two independent lines of Anemia.)

Erect fertile pinnae (I) and their origin approximate to the sterile pinnae (J) are further modifications. Fertile pinnae with at least a trace of lamina are closer to the condition of vegetative pinnae than those in which the lamina is lost entirely (K) and hence are most likely the more primitive.

L. SPORANGIAL SHAPE. In the oldest schizaeaceous fossils, the sporangia are oval, as they are in the modern genera of the family except Mohria. The large, spherical sporangium of Mohria is apparently an advanced condition.

M. SPORANGIAL APICAL PLATE CELLS. The cell walls of the apical plate are thick-walled in fossil Schizaeaceae, Mohria, and two subgenera of Anemia. Only members of subg. Anemia have thin walls.

N-P. SPORES. Spores of subg. Coptophyllum, Mohria, and the fossil Schizaeaceae all have ridges which are unornamented, broad, and relatively straight. Alternative conditions are found in the clavulate (N), narrow (O) ridges of subg. Anemia and undulating ridges (P) of subg. Anemiorrhiza.

SPECIES RELATIONSHIPS

In evaluating species relationships within the subgenus Coptophyllum, the same method of specialization indices based upon ground-plan correlations was employed. When applicable, values of 0.5 and 1.5 are given for intermediate or extremely advanced conditions respectively.

There are definite problems in applying this method to such a large number of closely interrelated species. Characters valuable in showing relationships in a particular group of species, for example, may have no phylogenetic or taxonomic significance in other groups of species. Therefore, such characters must often be left out to avoid confusion. There are enough characters used, however, to show the major trends and species groupings. Further data on species relationships are included in the species descriptions.

An explanation of the characters used is presented below.

A. LEAF HABIT. The flat rosette habit occurs only in the section Trochopteris.

B. FROND DIMORPHISM. The sterile and fertile fronds are essentially isomorphic except in section Coptophyllum.

C. RHIZOME HABIT. A horizontal rhizome is the rule for Mohria, subg. Anemiorrhiza, and most species of subg. Coptophyllum.

D. COMPACTNESS OF THE RHIZOME. Internodes are seemingly absent in Mohria and Anemia with the exception of subg. Anemiorrhiza. In subg. Coptophyllum, only Anemia tomentosa has a somewhat creeping rhizome.

E. RHIZOME HAIR COLOR. Maroon hair color is correlated with other primitive features in subg. Coptophyllum, orange color occurring only in isolated species groups, such as most of sect. Coptophyllum, A. karwinskyana and A. guatemalensis, part of A. villosa, and most of the African species of sect. Tomentosae.

F. RHIZOME HAIR LENGTH. In sect. Pachypoda the rhizome hairs are usually well over 1 cm long, whereas in nearly all other species the hairs, though dense, are relatively short, usually about 0.5 cm long.

G. STIPE DIAMETER. The slender stipe is correlated with species which have primitive features of the subgenus and is the general condition for ferns in general. The stipe is considered "stout" when it attains a diameter of 2 mm or more with a length less than about 40 cm.

H. CROSS SECTION OF STIPE. A flattened stipe is found in several unrelated taxa of subg. Coptophyllum, but it occurs in no other groups in the genus nor in Mohria.

I. STIPE PIGMENTATION. Stipes in Mohria and subg. Coptophyllum generally dry to a yellow or light brown color. A purple pigmentation occurs only in A. ferruginea and A. tomentosa var. anthriscifolia and is construed as a derived condition.

J. RACHIS-PINNA ORIENTATION. The peculiar downward-pointing pinnae of A. retroflexa are unique. No suggestion of such a condition is found in any other species of Anemia or in Mohria.

K. BLADE OUTLINE. The deltoid-ovate outline of the blade is typical for almost all species of Anemia including the primitive groups of subg. Coptophyllum. A more elongate, linear ovate outline is found in the A. villosa species-group.

L. FROND HEIGHT. A height of less than 10 cm in the sterile fronds is considered an advanced condition in subg. Coptophyllum. Plants 20 to 60 cm tall are most common in the genus and Mohria. Although this measurement appears to be arbitrary, it separates entire groups which are specialized in other features.

M. BLADE DISSECTION. Fronds, both in Mohria and in most species of subg. Coptophyllum, are bipinnate or bipinnate-pinnatifid, and deviations from this are considered specialized.

N. LAMINA BREADTH. Only in certain members of sect. Coptophyllum is the segment lamina reduced to a width of 0.5 mm.

O. LAMINAR TEXTURE. A coriaceous lamina is found in various sections of subg. Coptophyllum, but in the other three genera of the family and in ferns in general a more chartaceous texture is the most widespread.

P. INDUMENT OF THE BLADE. In most species of Anemia and Mohria the lamina is pilose to hirsute on both surfaces, and this type of pubescence is correlated with other primitive features. The two trends from this condition are tomentose or lanose lamina on the one hand (P^1) and to glabrous lamina on the other (P^2).

Q. SEGMENT MARGIN. In sect. Anemiaebotrys the margin of the segments is dentate with a single vein running to the apex of each tooth. This condition is found also in Mohria and is taken as the fundamental condition for Anemia. The other sections have lost this character.

R. MARGINAL SPICULES. Marginal spicules occur only in certain species with coriaceous leaves and hence are correlated with other advanced characters.

S. SHAPE OF EPIDERMAL CELLS. In the genus Mohria and most groups of Anemia subg. Coptophyllum the epidermal cell walls are somewhat lobed. Deviations have been in three directions: shallowly undulating walls on the upper epidermis (S^1), lobes somewhat squarish (S^2), and arms more slender (S^3).

T. STOMATAL POSITION. Nearly all ferns and higher plants have stomates located between two or more epidermal cells affixed to

the side of one epidermal cell, the subsidiary cell. The so-called "floating" stomate is found as a rule in the other two subgenera of Anemia, but in only two sections of subg. Coptophyllum.

U. TRICHOME ATTACHMENT. The large type of unicellular hair has a subbasal attachment in nearly all species of subg. Coptophyllum. It has a medial attachment in only one species.

V-X. FERTILE PINNAE. Since the fertile pinnae are assumed to be merely modifications of vegetative pinnae, resemblances to the latter are most probably primitive, and similarly, deviations from characteristics of vegetative pinnae are construed as specialized. Erect habit (V), position approximate to the sterile pinnae (W), and length exceeding the sterile blade (X) are three specializations found in subg. Coptophyllum.

Y. SPORE SIZE. An average spore diameter of over 85 μ is considered specialized, since it is thought to be due largely to polyploidy.

Z. SPORE ANGLE PROTUBERANCES. In nearly all species of subg. Coptophyllum and Mohria, the spore angles have protuberances. They are lacking in only a few species.

1. VERRUCULATE RIDGES. Ridges are slightly warty or verruculate in several species of sect. Tomentosae, the extreme condition being found in A. flexuosa. It is thus correlated with other advanced features since it is not found in any of the primitive species nor in Mohria nor other groups of Anemia.

2. RIDGE MEDULLA. The spongy ridge medulla occurs chiefly in sect. Tomentosae. Most other sections lack it, and it is not found in other groups of Anemia or Mohria.

3. RIDGE PATTERN. For the most part the spore ridges run parallel to one another. Only in A. aethiopica are the ridges regularly anastomosing.

Plate XI shows several major evolutionary lines within the subgenus from which six sections have been defined. The two most primitive species, Anemia aspera and A. perrieriana, comprise the section Anemiaebotrys and probably closely resemble the ancestors of the subgenus. Arising from sect. Anemiaebotrys is a group of four species (sect. Pachypoda) which is characterized by a large rhizome, flattened stipe, coriaceous texture, and spicular perine.

Continuing in a clockwise direction on the diagram, the next evolutionary line, sect. Coptophyllum, is a group of small, coriaceous plants with floating stomates, marginal spicules, and tendencies to frond dimorphism and great reduction of the laminar tissue. This line reaches its climax in A. buniifolia and A. millefolia.

The section Adetostoma (A. smithii, A. brandegeea, and A. intermedia) represents another line of relatively small plants with floating stomates. The lamina is chartaceous, resembling the more generalized species of subg. Coptophyllum, but the fertile pinnae are held horizontally or only suberect.

The rosette-forming species, A. eximia and A. elegans (sect. Trochopteris), comprise a different line of specialization. The possible relationship of this group to the A. (sect. Tomentosae) villosa group of species is indicated by the dotted line. Although A. eximia is somewhat intermediate between the extreme form of A. elegans and a more generalized form of the subgenus, the precise affinities of sect. Trochopteris

are not clear. Similarities in habit, spores and trichomes suggest a relationship with A. trichorrhiza, another species of doubtful affinities.

According to correlations between sections, the first five sections are relatively isolated. Each possesses unique and often striking morphological features, and no hybrids have yet been found involving these species, all of which are distinct. The most difficult problem lies in finding the relationships between sections. On the other hand, the remaining section, Tomentosae, with twenty-three species, has many interspecific problems. This section comprises not only the bulk of the species of the subgenus, it also includes all of the widespread species. Generally these are larger plants, the fertile pinnae are held erect, and the spore ridges contain a spongy medulla. Most of the species appear to be closely related, as evidenced both by their morphological features and their ability to hybridize. Several species groups can be distinguished, but there are two major complexes which are especially problematic, those of A. villosa and A. tomentosa-ferruginea. On the phylogenetic diagram, these are designated by heavy lines.

TAXONOMIC REVISION

Anemia

Anemia Swartz, Syn. Fil. 6, 155. 1806. (nom. cons.)
Ornithopteris Bernhardi, Schrad. Neu. Journ. 1(2):40. 1806.
Aneimia Swartz, corr. Kaulfuss, Enum. Fil. 51. 1824.
Anemidictyon J. Smith in Hooker, Gen. Fil. t.103. 1841.
Trochopteris Gardner, London Jour. Bot. 1:74. 1842.
Coptophyllum Gardner, London Jour. Bot. 1:133. 1842.
Aneimidictyum J. Smith, corr. Presl, Suppl. Tent. Pterid. 91. 1845.
Anemirhiza J. Smith in Seemann, Bot. Voy. Herald 6:243. 1854.
Aneimiaebotrys Fée, Crypt, Vasc. Brés. 1:267. 1869.
Hemianemia (Prantl) Reed, Bol. Soc. Brot. II. 21:154. 1948.

Rhizome horizontal or oblique, compact or short-creeping; indument of hairs; fronds erect and spreading, rarely forming a flat rosette, pinnately divided; sporangia usually restricted to lowermost pair of pinnae but fronds occasionally dimorphic; fertile pinnae held erect, rarely horizontally; sporangia in two rows on ultimate segments of fertile pinnae, suberect, sessile, subglobose to oval; spores tetrahedral to globose, striate.

Distribution. Tropics and subtropics of America, Africa, and southern India.

Type species. Anemia phyllitidis (L.) Swartz.

Key to the Subgenera of Anemia

1. Rhizome creeping, clothed with dark brown hairs; fronds distichous; lamina coriaceous; multicellular laminar hairs nonglandular; spore ridges undulating, medullate. . . . . 1. Anemiorrhiza

1. Rhizome compact, clothed with orange or maroon hairs; fronds polystichous; lamina chartaceous or coriaceous; multicellular laminar hairs glandular; spore ridges straight, solid or spongy-medullate. 2

2. Leaves usually once pinnate; stomates floating; fertile pinnae approximate to sterile pinnae; spore ridges clavulate (smooth in sects. Oblongifoliae and Hirsutae); striae broader than ridges (narrower in sect. Oblongifoliae). . . . 2. Anemia

2. Leaves usually pinnate-pinnatifid to tripinnate; fertile pinnae remote or approximate to sterile pinnae; stomates attached, rarely floating; spore ridges smooth; striae narrower than ridges . . . . . 3. Coptophyllum

Subgenus Coptophyllum

Aneimia subg. Coptophyllum (Gardner) Presl, Suppl. Tent. Pterid. 79. 1845.
Trochopteris Gardner, London Jour. Bot. 1:74. 1842.
Coptophyllum Gardner, London Jour. Bot. 1:133. 1842.
Aneimia subg. Trochopteris (Gardner) Sturm in Martius, Fl. Bras. 1(2):187. 1859.
Aneimiaebotrys Fée, Crypt. Vasc. Bres. 1:267. 1869.
Aneimia subg. Hemianeimia Prantl, Schiz. 86. 1881.
Hemianemia (Prantl) Reed, Bol. Soc. Brot. II. 21:154. 1948.

Rhizome horizontal, rarely ascending, compact, rarely short-creeping; hairs maroon or orange; stipe usually dull yellow, rarely darkly pigmented or bright yellow; blade usually deltoid-ovate, bipinnate to bipinnate-pinnatifid, chartaceous, pilose or hirsute; marginal spicules rare; fertile pinnae held erect, rarely horizontally, in a position either remote or approximate to the sterile pinnae; ultimate segments of fertile pinnae with a lamina about 1 mm broad; spores tetrahedral to globose, large (most 65-110 μ in diameter); angle protuberances conspicuous to essentially lacking; ridges usually smooth and straight; striae narrower than the ridges.

Distribution. Same as for the genus but rare in the West Indies.

Type species. Anemia buniifolia (Gardner) Moore.

Key to the Sections of Subgenus Coptophyllum

1. Fronds forming a flat rosette. . . . . E. Trochopteris

1. Fronds ascending and spreading. 2

2. Fronds dimorphic; marginal spicules usually present; stomates floating. . . . . C. Coptophyllum

2. Fronds isomorphic; marginal spicules usually absent; stomates attached (floating in sect. Adetostoma). 3

3. Fertile pinnae sessile or subpetiolate, horizontal to suberect. . 4

4. Margin denticulate; rhizome hairs maroon; stomates attached. . . . . A. Anemiaebotrys

4. Margin entire; rhizome hairs orange or orange-red; stomates floating. . . . . D. Adetostoma

3. Fertile pinnae petiolate, erect 5

5. Lamina coriaceous; stipe flattened; spores with spicular perine. . . . . B. Pachypoda

5. Lamina chartaceous or coriaceous; stipe terete; spores with smooth perine. . . . . F. Tomentosae

Key to the Species of Subgenus Coptophyllum

1. Sporangia distributed over whole fertile frond; blade finely dissected into linear segments (ca. 0.5 mm broad). 2

2. Fronds strictly pinnate in plan; fertile pinnae subsessile; spores 65-107 μ. . . . . 8. A. millefolia

2. Fronds somewhat dichotomously branching; fertile pinnae petiolate; spores 45-59 μ. . . . . 7. A. buniifolia

1. Sporangia limited to basal pinnae of fertile frond; blade coarsely dissected into broad segments (broader than 1 mm). 3

3. Fronds forming a flat rosette 4

4. Leaves 1-2 cm long, pinnatifid, nearly sessile. 14. A. elegans

4. Leaves mostly 3-8 cm long, pinnate to pinnate-pinnatifid, petiolate. . . . . 15. A. eximia

3. Fronds erect and spreading. 5

5. Fertile pinnae held horizontally. 6

6. Segment margin dentate; spore perine slightly spiculate. 7

7. Fronds 30-100 cm long; stipe flattened only at the base; spores 78-91 μ; spore angles protruding. 1. A. aspera

7. Fronds 9-23 cm long; stipe flattened throughout its length; spores 62-68 μ; spore angles rounded. 2. A. perrieriana

6. Segment margin entire or slightly serrate; spore perine smooth. 8

8. Lamina coriaceous, lanose below, subglabrous above. 6. A. trichorrhiza

8. Lamina chartaceous, pilose to tomentose. 9

9. Blade pinnate to pinnate-pinnatifid; rhizome hairs maroon; West Africa. . . . . 16. A. sessilis

9. Blade pinnate-pinnatifid to bipinnate; rhizome hairs orange; Mexico. 10

10. Fronds 2-6 cm long. . . . . 13. A. brandegeea

10. Fronds 9-16 cm long. . . . . 12. A. intermedia

5. Fertile pinnae held erect or suberect. 11

11. Plants from Africa or India. 12

12. Stipe flattened. 13

13. Blade bipinnate, coriaceous; rhizome hairs maroon; spore ridges parallel; Madagascar. . . . . 5. A. lanipes

13. Blade bipinnate-pinnatifid, chartaceous; rhizome hairs orange; spore ridges anastomosing; Ethiopia. 19. A. aethiopica

12. Stipe approximately terete. 14

14. Blade bipinnate-pinnatifid to tripinnate; spore angles rounded; Madagascar. . . . . 17. A. madagascariensis

14. Blade bipinnate to bipinnate-pinnatifid; spore angles protruding; Africa or India. 15

15. Rhizome apex ascending and covered with petiole bases; stipe stout (ca. 2 mm broad). 16

16. Fronds 11-37 cm tall; blade bipinnate to bipinnate-pinnatifid, hirsute to tomentose; India. . . . . 20. A. wightiana

16. Fronds 26-60 cm tall; blade bipinnate-pinnatifid, pilose to hirsute; Nigeria. 23. A. nigerica

15. Rhizome apex horizontal and exposed; stipe slender (1.0-1.5 mm broad) or stout, pilose to hirsute; Africa. 17

17. Fertile pinnae remote to subapproximate to the sterile; spore angle protuberances inconspicuous. . 18. A. schimperiana

17. Fertile pinnae approximate to the sterile; spore angle protuberances conspicuous. 18

18. Rhizome hairs orange; stipe slender (ca. 1 mm broad); fertile pinnae glabrous. . . . . 21. A. simii

18. Rhizome hairs maroon; stipe stout (ca. 2 mm broad); fertile pinnae densely pubescent. . . . . 22. A. angolensis

11. Plants from Latin America. 19

19. Blade once pinnate or pinnate-pinnatifid. 20

20. Pinnae mostly unlobed. 21

21. Venation pinnate; costa present; stipe terete; rhizome hairs less than 1 cm long. 22

22. Rhizome apex horizontal and exposed; rhizome hairs maroon; blade coriaceous; fertile pinnae approximate to the sterile. . . . . 27. A. blechnoides

22. Rhizome apex ascending and clothed with petiole bases; rhizome hairs orange; blade chartaceous; fertile pinnae remote from sterile. . 25. A. organensis

21. Venation flabellate; costa lacking; stipe flattened; rhizome hairs ca. 1.5 cm long. 23

23. Stipe longer than 9 cm; pinnae orbicular; lamina glabrous. . . . . 3. A. gardneri

23. Stipe less than 5 cm long; pinnae oblong; lamina tomentose. . . . . 4. A. lanuginosa

20. Pinnae lobed or pinnatifid. 24

24. Sterile fronds less than 10 cm long; stipe dark brown. . . . . 10. A. glareosa

24. Sterile fronds longer than 10 cm; stipe yellow or light brown, rarely dark brown. 25

25. Blade oblong to linear, chartaceous to subcoriaceous; stipe slender (1-2 mm broad). . . . . 24. A. villosa

25. Blade deltoid-ovate to oblong, coriaceous; stipe stout (ca. 2 mm broad). . . . . 26. A. imbricata

19. Blade bipinnate or more dissected. 26

26. Most pinnae of a single frond catadromous; spore angles rounded; Mexico and Central America. 27

27. Rhizome hairs chestnut-colored; lower one-third of stipe dark brown; blade bipinnate-pinnatifid to tripinnate-pinnatifid. . . . . 38. A. colimensis

27. Rhizome hairs orange; stipe yellow throughout; blade bipinnate to tripinnate. 28

28. Blade bipinnate or bipinnate-pinnatifid; segments ovate-obtuse. . . . . 36. A. karwinskyana

28. Blade bipinnate-pinnatifid to tripinnate; segments ovate to elongate-ovate. . . . . 37. A. guatemalensis

26. Most pinnae of a single frond anadromous; spore angles with conspicuous protuberances; mostly in South America. 29

29. Rhizome apex ascending to erect and clothed with petiole bases; western South America. 30

30. Blade over 15 cm long; stipe yellow, stout (1-2 mm broad); fertile pinnae erect, long-petioled. . . . 32. A. flexuosa

30. Blade ca. 10 cm long; stipe dark brown, slender (less than 1 mm broad); fertile pinnae suberect, short-petioled. . . . . 11. A. smithii

29. Rhizome apex horizontal and exposed; tropical America. . 31

31. Rhizome over 2 cm thick; stipe flattened; pinnae retroflexed. . . . . 28. A. retroflexa

31. Rhizome less than 1.5 cm thick; stipe terete; pinnae horizontal or ascending. 32

32. Frond bipinnate-pinnatifid to tripinnate, lanose. 35. A. myriophylla

32. Frond bipinnate to bipinnate-pinnatifid; subglabrous to hirsute, rarely tomentose. 33

33. Rhizome hairs orange. 34

34. Blade less than 6 cm long, coriaceous; fertile pinnae sessile, often more than 1 pair. 9. A. rutifolia

34. Blade usually longer than 10 cm. 35

35. Blade bipinnate, rarely bipinnate-pinnatifid; spore diam. under 85 μ. . . . . 33c. A. tomentosa var. australis

35. Blade bipinnate-pinnatifid; spore diam. greater than 85 μ. . . 36

36. Fertile pinnae remote or approximate to sterile; spores mostly uniform. . . . . 33d. A. tomentosa var. mexicana

36. Fertile pinnae approximate to sterile; spores often irregular and abortive. 37

37. Stipe slender (1.0-1.5 mm broad), at least partially darkly pigmented; blade deltoid; segment lobes shallow, acute. . . . . 33b. A. tomentosa var. anthriscifolia

37. Stipe stout (ca. 2 mm broad), yellow; blade ovate; segment lobes deep, rounded. 33a. A. tomentosa var. tomentosa

33. Rhizome hairs red to maroon. 38

38. Frond ca. 30 cm long; blade coriaceous; fertile pinnae approximate or subapproximate to sterile. 39

39. Stipe stout, yellow to dark brown; fertile pinnae "bushy," only slightly exceeding the sterile blade; spores normal. 26. A. imbricata

39. Stipe slender, dark purplish; fertile pinnae slender, greatly exceeding the sterile blade; many spores irregular and abortive. 40

40. Blade bipinnate, rarely bipinnate-pinnatifid; segments obtuse. . . . . 34a. A. ferruginea var. ferruginea

40. Blade bipinnate-pinnatifid; segments acute to acuminate. . . . . 34b. A. ferruginea var. ahenobarba

38. Frond ca. 45 cm long; blade chartaceous to subcoriaceous; fertile pinnae remote from sterile. 41

41. Blade bipinnate-pinnatifid, chartaceous. 42

42. Attachment of large unicellular trichomes medial; spore diam. less than 80 μ; s.e. South America. 29. A. simplicior

42. Attachment of large unicellular trichomes subbasal; spore diam. greater than 80 μ; Central America. 31. A. bartlettii

41. Blade bipinnate, chartaceous to subcoriaceous. 30. A. raddiana

A. Section Anemiaebotrys

Anemia subg. Coptophyllum sect. Anemiaebotrys (Fée) Mickel, stat. nov.
Aneimiaebotrys Fée, Crypt. Vasc. Brés. 1:267. 1869.
Hemianemia subg. Aneimiaebotrys (Fée) Reed, Bol. Soc. Brot. II. 21:154. 1948.

Rhizome clothed with maroon hairs; fronds bipinnate to tripinnate, chartaceous; margin coarsely dentate; fertile pinnae horizontal, subpetiolate, remote from sterile pinnae; spore perine usually somewhat spiculate.

Type species: Anemia aspera (Fée) Baker.

1. Anemia aspera (Fée) Baker, Jour. Linn. Soc. 14:27. 1873 (Plate XII, Fig. A).
   Anemiaebotrys aspera Fée, Crypt. Vasc. Brés. 1:267. t. 78 f. 2. 1869.
   Hemianemia aspera (Fée) Reed, Bol. Soc. Brot. II. 21:157. 1948.[1]

Rhizome horizontal compact, 1-2 cm thick; hairs maroon; fronds caespitose; stipe terete, 12-58 cm long, 1-2 mm thick, dull yellow, pilose; blade deltoid-ovate, bipinnate-pinnatifid to tripinnate, chartaceous, 18-40 cm long; pinnae 12-15 pairs, either mostly catadromous or mostly anadromous; pinnules lanceolate, pinnatifid to pinnate, short-petiolate; segments ovate, pilose; margin dentate; fertile pinnae horizontal, remote from sterile pinnae, about the same length as the lowermost sterile pinnae; spores 78-91 μ, tetrahedral, the angle protuberances conspicuous, the ridges smooth, spongy-medullate; the perine spiculate.

Distribution. Rio de Janeiro, Brazil. (Pl. VII, Fig. A).

Type collection. "Serra os Orgaos, an Morro Quemado, chemin dos Macacos, Glaziou 3821." The type is probably either at P or BR. Although Fée worked at P, important Glaziou collections are located in both herbaria. The specimen I have seen from BR bears no designation of being the type.

Specimens examined.[2] BRAZIL. RIO DE JANEIRO; Bôa Vista, Samare, Brade 8560 (NY, UC); Corcovado, Luetzelburg 258 (BM, MICH, UC, US), Webb, in 1867-68 (NY); Morro Queimado, Brade 8568a (DEN), Brade 10884 (R), Brade 16860 (MICH), Brade, in 1933 (RB no. 33296) (RB, US), Schwacke 812 (RB), entre la Tijuca et la Gavia, Glaziou 4460 (P); Serra do Cariacá, Brade, 18 Nov 1928 (R); Tijuca, Alston 8968 (BM); Glaziou 3821 (BR, isotype).

[1] Names not validly published have been omitted from the species synonymy. Many of these can be found in Moore's Index Filicum (1857) and in Martius' Flora Brasiliensis (1859).

[2] Following is a list of herbaria from which specimens have been borrowed. Abbreviations are those found in Lanjouw and Stafleu (1956):

Discussion. Probably the most striking feature of A. aspera is the close resemblance of the fertile pinnae to sterile ones in their horizontal habit and their architecture. In this respect and in other morphological features this species is the least specialized of the subgenus.

The frequent catadromous character led to early confusion with A. guatemalensis, which was included with it. However, on the basis of other morphological characters, such as spores and rhizome hair color, it seems more likely that the A. guatemalensis group of species arose from the section Tomentosae with affinities to A. tomentosa.

The spores of A. aspera have the most conspicuous angle protuberances of any modern species of Anemia, and in this feature resemble species of the fossil form genus Appendicisporites.

Although only the base of the stipe is flattened in A. aspera, this character and the spiculate perine strongly suggest a relationship of sect. Anemiaebotrys to sect. Pachypoda.

2. Anemia perrieriana C. Chr., Cat. Pl. Mad. Pter. 65. 1931 (nomen); Dansk Bot. Ark. 7:178. t. 72, f. 5, 6. 1932 (Pl. XII, Fig. B). Hemianemia perrieriana (C. Chr.) Reed, Bol. Soc. Brot. II. 21: 157. 1948.

Rhizome horizontal, up to 1 cm thick; hairs maroon; fronds caespitose; stipe flattened throughout its length, 4-10 cm long, less than 1 mm thick, dull yellow, pilose; blade elongate deltoid, pinnate-pinnatifid to bipinnate, chartaceous, 5-13 cm long; pinnae 7-11 pairs, somewhat catadromous; pinnules broadly adnate, oblong, pilose; margin dentate; fertile pinnae horizontal, subpetiolate, remote from sterile pinnae, about same length as the lowermost sterile pinnae; spores 62-68 μ, tetrahedral-globose, the angle protuberances inconspicuous, the ridges smooth, solid, the perine slightly spiculate.

Distribution. Madagascar (Pl. VII, Fig. A).

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2 (cont.)

BM	British Museum (Natural History), London, Great Britain
BR	Jardin Botanique de l'Etat, Bruxelles, Belgium
FI	Herbarium Universitatis Florentinae, Istituto Botanico, Firenze, Italy
G	Conservatoire et Jardin botaniques, Genève, Switzerland
GH	Gray Herbarium of Harvard University, Cambridge, Massachusetts
HBR	Herbario "Barbosa Rodrigues," Itajaí, Santa Catarina, Brazil
K	The Herbarium and Library, Royal Botanic Gardens, Kew, Richmond, Surrey, Great Britain
MICH	University Herbarium, University of Michigan, Ann Arbor, Michigan
MO	Missouri Botanical Garden, Saint Louis, Missouri
NY	The New York Botanical Garden, New York, New York
P	Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris, France
R	Divisão de Botânica do Museu Nacional, Rio de Janeiro, Brazil
RB	Jardin Botânico, Rio de Janeiro, Brazil
S-PA	Palaeobotanical Department, Swedish Museum of Natural History, Stockholm, Sweden
UC	Herbarium of the University of California, Berkeley, California
US	U.S. National Museum, Smithsonian Institution, Washington, D.C.

Type collection. "Bois rocailleux et très secs, Massif de Manongarivo, vers 1000 m. d'alt., sur gneiss, avril 1909, Perrier 7485." I have seen a photograph of the holotype, which is in the Christensen herbarium at BM.

Specimens examined. MADAGASCAR. Manongaite, Sambirano, Perrier 7484 (BM, P), Perrier 7485 (Bm, isotype).

Discussion. This species looks very much like small specimens of A. aspera, and it is noteworthy that these two most primitive species are found on different continents. Apparently this primitive form with horizontal fertile pinnae was widespread before the fertile pinnae became erect in the evolution of the subgenus.

B. Section Pachypoda

Section Pachypoda Mickel, sect. nov.

Rhizomate horizontali, crasso (1.0-2.5 cm), pilis longis atrorufis vel aurantiacis vestito; petiolo lato (1-3 mm), planato; foliis pinnatis vel bipinnatis; lamina coriacea; cellulis epidermis superioris cum marginibus undulatis potius quam profunde invaginatis; sporis perinio spiculatis.

Type species. Anemia gardneri Hooker.

3. Anemia gardneri Hooker, Ic. Plant. t. 190. 1837 (Pl. XIII, Fig. A).
Anemia glaziovii Fée, Crypt. Vasc. Brés. 1:207. t. 74, f. 2. 1869.
Anemia gardneriana Christ, Farnkr. 346. 1897, non Presl, 1845.
Hemianemia gardneri (Hooker) Reed, Bol. Soc. Brot. II. 21:160. 1948.

Rhizome horizontal, compact, 1.5-2 cm thick; hairs maroon to orange; fronds caespitose; stipe flattened, 9-23 cm long, 2-3 mm broad, yellow, pilose to subglabrous; blade oblong-ovate, pinnate, coriaceous, 8-20 cm long; pinnae 4-8 pairs, oblong-orbiculate, glabrous on both surfaces; margin slightly denticulate; fertile pinnae erect, petiolate, remote to subapproximate to the sterile pinnae, not exceeding the sterile blade in height; spores 88-117 μ, tetrahedral-globose, the angles rounded, the ridges low and inconspicuous, smooth, solid, the perine spiculate.

Distribution. Rio de Janeiro, Brazil (Pl. VII, Fig. A).

Type collection. Brazil, Gardner n. 4.

Specimens examined. BRAZIL. RIO DE JANEIRO: Corcovado, Brade 15319 (RB), Brade, June 1928 (R no. 16696)(R, UC); Frade de Macabé, Brade 15819 (RB); Pico del papagaio, vostri da pic de Tijuca, Glaziou 2058 (BR, P); Organ Mountains, Pedra Maria Autonieta, Wagner, 17 June 1901 (P); Sta. Madalena, Pedra das Flores, Santos Lima & Brade 13181 (RB); Sta. Madalena, Serra de Jumaca, Santos Lima, Nov. 1935 (RB no. 27804) (RB); Serra do Couto, Glaziou 3175 (BR, P); Tijuca, Brade 8583 (DEN, NY, UC), Ule, in Sept. 1899 (R no. 1417) (R); Pico de Tijuca, Brade 12551 (RB), Brade 16855 (G, MICH, NY), Brade, 2 June 1929 (R no. 21389) (R), Gardner 4 (K, type; BM), Glaziou 1872 (P); White, in 1870 (BM).

Discussion. This and A. lanuginosa appear to be the most highly specialized species in this evolutionary line. They are both only once

pinnate and the perine is the most spiculate of any in the group, with spicules up to 7 μ in height.

The fact that members of this small section are found both in the New Old Worlds suggests an early origin of the group.

4. Anemia lanuginosa Bongard ex Sturm in Mart., Fl. Bras. 1(2):210. 1859 (Pl. XIII, Fig. B).
Anemia oblongifolia Swartz var. lanosa Baker, Jour. Bot. 1885:218.
Anemia gardneriana sensu Christ, Bull. Herb. Boiss. II. 2:694. 1902, non Presl, 1845.
Anemia gomesii Christ, Bull. Herb. Boiss. II. 7:891. 1907.
Hemianemia lanuginosa (Bongard) Reed, Bol. Soc. Brot. II. 21:160. 1948.

Rhizome horizontal, 1.5-2.5 cm thick; hairs maroon; fronds caespitose; stipe somewhat flattened, 1-5 cm long; 1-2 mm broad, yellow, villous; blade oblong-ovate, pinnate, coriaceous, 5-12 cm long; pinnae 7-13 pairs, oblong, entire to crenate, subglabrous to tomentose on both surfaces; fertile pinnae petiolate, erect, remote from the sterile pinnae, shorter than the sterile blade; spores 75-91 μ, tetrahedral-globose, the angles rounded, the ridges low and inconspicuous, smooth, solid, the perine spiculate.

Distribution. Minas Gerais, Brazil (Pl. VII, Fig. A).

Type collection. "In prov. Minarum, Serra de Ouro branco: Sellow (Herb. Berol. B. n. 672, c. 9); ad S. Jose (Herb. Kunzei)." Since I have seen specimens of neither collection, I have no basis upon which to designate a lectotype. The Kunze herbarium at Leipzig, however, was destroyed during World War II.

Specimens examined. BRAZIL. MINAS GERAIS: Carmo do Rio Claro, Fazenda Alegria, Emygdio 591 (R); Cons. Matta, Lama Preta, Brade 13952 (RB); Diamantina, Brade 13953 (G, RB); Ouro Preto, Badini 35 (R); Serra de Ouro Preto, Marco, Damazio 1849 (P); Ouro Preto, Damazio, in 1907 (US); Serra da Caraça, Ule 263 (NY, R); Serra de São Thomé das Letras, Pico do Gaviao, Silveira 110 (R); São Thomé das Letras, Baipendi, Brade 20474 & Apparicio (G, MICH, NY); Serra do Cipó, Barreto (4436) & Brade 14402 (G, MICH, NY), da Costa 135 (R), Damazio 1952 (DEN, NY, RB, S-PA, UC), Damazio, in July 1907 (R no. 18328) (R); Serra do Cipó, Palácio, Duarte 2031 (G, MICH); vaccaria n. of Bello Horizonte, Serra do Cipó, Conecica, Foster & Foster 612 (US); Monte Claros, Serra do Calistro, Markgraf, Barreto, & Brade, 10 Nov. 1938 (RB no. 39649) (RB); Serra do Frazão, Schwacke 14885 (MICH); Serra do Itatiaya, prope Chapada, 12 May 1895, Magalhães & Schwacke 2485 (P), as 4285 (R), s.n. (RB); São João del Rey, Serra do Lenheiro, Agua Geral, Barreto 4768 (RB); Claussen 328 (FI); Glaziou 16644 (NY); Glaziou 20161 (NY, US); Raddi 13 (US).

Discussion. The nearest relative of A. lanuginosa is A. gardneri, but they can readily be distinguished by the densely hairy frond and very short stipe of A. lanuginosa. It was in A. lanuginosa that Bolchovitina (1959) made the first report of a perine in the spores of Anemia, and I also first noticed it in this species. Both in sect. Pachypoda and sect. Coptophyllum the perine falls off quite readily.

5. Anemia lanipes C. Chr., Cat. Pl. Mad. Pter. 65. 1931 (nomen); Dansk Bot. Ark. 7:177. t. 71, Fig. 1-3. 1932 (Pl. XIV, Fig. A).
Hemianemia lanipes (C. Chr.) Reed, Bol. Soc. Brot. II. 21:162. 1948.

Rhizome horizontal, 1-2 cm thick; hairs maroon; fronds caespitose; stipe flattened, 9-26 cm long, 2-4 mm broad, yellow, villous but hairs readily deciduous; blade deltoid-ovate, bipinnate, coriaceous, 6-16 cm long; pinnae 8-10 pairs; pinnules broadly adnate, ovate-obtuse, entire, crenate to lobed, glabrous above, subglabrous below; fertile pinnae petiolate, erect, subapproximate to the sterile pinnae, not exceeding the sterile blade; spores 84-98 μ, tetrahedral-globose, the angle protuberances inconspicuous, the ridges smooth, solid, the perine spiculate.

Distribution. Madagascar (Pl. VII, Fig. A).

Type collection. "Environs de Fort-Dauphin: forêt de Manantentely, sur rochers granitiques, vers 300 m., 22 septembre 1928, Humbert 5808." I have seen a photograph of the holotype, which is in the Christensen herbarium at BM.

Specimens examined. MADAGASCAR. Ambatofinandrahana, Decary 15172 (P); Fort Dauphin, Fôret de Manantentely, Humbert 5808 (BR, P, isotypes); Fort Dauphin, Scott Elliot 2798 (K); Mt. Ibity, Perrier 18496 (BM, BR).

Discussion. The relationship of A. lanipes to the other species of this section has not been recognized up to this time. The outstanding difference between it and A. lanuginosa and A. gardneri is in the degree of dissection of the frond, but in all other respects is closely allied to these species. It is the only member of the section in the Old World.

6. Anemia trichorrhiza Gardner in Hooker, Ic, Pl. t. 876. 1852 (Pl. XIV, Fig. B).
Anemia nana Baker, Engl. Bot. Jahrb. 17:522. 1893.
Anemia trichorhiza var. paraguariensis Hassler, Trab. Inst. Bot. Farm. Buenos Aires 45:83. 1928.
Anemia tomentosa var. trichorhiza (Gardner) Farwell, Am. Midl. Nat. 12:307. 1931.
Hemianemia trichorhiza (Gardner) Reed, Bol. Soc. Brot. II. 21:157. 1948.
Hemianemia nana (Baker) Reed, Bol. Soc. Brot. II. 21:159. 1948.

Rhizome horizontal, 0.5-1.3 cm thick; hairs maroon; fronds caespitose; stipe flattened, up to 4 cm long, 1-2 mm broad, yellow to dark brown, lanose; blade deltoid-ovate, pinnate-pinnatifid to bipinnate, coriaceous, 2.5-8 cm long; pinnae 8-12 pairs; pinnules broadly adnate, deltoid-obtuse, lanose especially on the lower surface; fertile pinnae short-petiolate, horizontal to suberect, remote from the sterile pinnae, longer than the lowermost sterile pinnae, and sometimes exceeding the sterile blade; spores 61-78 μ, tetrahedral-globose, the angle protuberances poorly developed, the ridges smooth, solid, the perine smooth.

Distribution. Paraguay and the states of Minas Gerais, Goias, and Matto Grosso, Brazil (Pl. VII, Fig. A).

Type collection. Dry rocks, summit of Sierra de Natividade, Brazil, Feb. 1841, Gardner 4080.

Specimens examined. BRAZIL. GOIAS: Goias, Morro S. Francisco, Macedo 3525 (RB p.p.); Serra Dourada, Ule 539 (R), Glaziou 22626 (RB p.p.); Gardner, in 1841 (RB no. 12865) (RB). MATTO GROSSO: Cuiaba, Schwacke 5000 (RB); Serra da Chapada, Malme 3351 (BM); Serra da Chapada, pr. Bocca da Serra, Malme, 6 Nov. 1903 (R no. 21559) (R); Burchell 7043 (K, P); Burchell 7881 (K). MATTO GROSSO-ACRE: Casa de Pedra (Luiha de Leste), Hoehne 3804 (R). MINAS GERAIS: summit of Serra de Natividade, Gardner 4080 (K, type; BM, NY), Glaziou 20160 (K); Glaziou 15794 (NY, P, US).

PARAGUAY. Cerro Pelada, Jorgensen 4393 (F p.p., MO p.p., US).

Discussion. The relationships of A. trichorrhiza are not clear. Prantl could not place it in any of his sections. I believe it is best placed in sect. Pachypoda on the basis of its coriaceous texture, flattened stipe, long rhizome hairs, and wavy cell walls of the upper epidermis. However, in characters such as its small fronds in a subrosette, heavy pubescence, and small spores which lack a spicular perine, A. trichorrhiza resembles A. (sect. Trochopteris) eximia more closely than it does the other members of sect. Pachypoda.

C. Section Coptophyllum

Coptophyllum Gardner, London Jour. Bot. 1:133. 1842.
Aneimia subg. Coptophyllum (Gardner) Presl, Suppl. Tent. Pterid. 79. 1845.
Aneimia subg. Hemianeimia sect. Gardnerianae Prantl, Schiz., 87. 1881.
Anemia subg. Hemianeimia sect. Millefoliae Prantl, Schiz., 87. 1881.
Hemianemia subg. Coptophyllum sect. Eu-Coptophyllum Reed, Bol. Soc. Brot. II. 21:158. 1948.
Hemianemia subg. Coptophyllum sect. Rutaefoliae Reed, Bol. Soc. Brot. II. 21:159. 1948.
Hemianemia subg. Eu-Hemianemia sect. Gardnerianae (Prantl) Reed, Bol. Soc. Brot. II. 21:160. 1948.

Plants small, sterile fronds generally less than 10 cm tall; rhizome hairs usually orange; fronds dimorphic to subisomorphic; lamina usually greatly reduced, coriaceous; stomates mostly suspended or floating; marginal spicules often present; spore perine smooth.

Lectotype: Anemia buniifolia (Gardner) Moore. Christensen (1906) and subsequent authors have selected this species as the type of the genus Coptophyllum.

7. Anemia buniifolia (Gardner) Moore, Ind. Fil. 64. 1857 (Pl. XV, Fig. A).
Coptophyllum buniifolium Gardner, London Jour. Bot. 1:133. 1842.
Mohria buniifolia (Gardner) J. Smith, London Jour. Bot. 2:388. 1843.
Aneimia dichotoma Gardner ex Presl, Suppl. Tent. Pterid. 80. 1845.
Aneimia tenuifolia Presl, Abh. Böhm. Ges. V. 5:327. 1848.
Hemianemia buniifolia (Gardner) Reed, Bol. Soc. Brot. II. 21:158. 1948.

Rhizome horizontal, up to 7 mm thick; compact to short-creeping; hairs orange; fronds caespitose to scattered; stipe 1-5 cm long, ca. 0.5 mm thick, yellow to light brown, subglabrous; blade deltoid-ovate, tripinnate to quadripinnate, subcoriaceous, 3-10 cm long; pinnae 3-8 pairs, anadromous, petiolate and more or less dichotomously divided and with segments remote, giving the plant a lax appearance; segments ca. 0.5 mm broad; marginal spicules lacking; fertile fronds 4-15 cm tall; stipe 1-15 cm; blade 2-7 cm; pinnae petiolate, spreading; spores 45-59 μ, tetrahedral-globose, the angle protuberances inconspicuous, the ridges low, smooth, solid.

Distribution. Interior Brazil, Venezuela, Colombia (Pl. VIII, Fig. A).

Type collection. "In saxosis in summitate montis Serra de Natividade, prov. Goyazanae [Brazil], Gardner 4084."

Specimens examined. BRAZIL. GOIAS: Region of the Chapada dos Veadeiros, 7 km south of Veadeiros, Dawson 14588 (US); Serra de Natividade, Gardner 4084 (K, type). MATTO GROSSO: Alto Tapajos, Sick B-537 (RB); Cachoeira de São João da Barra, Kuhlmann 54 (NY, UC); Casa de Pedra, Hoehne 3816 (NY, UC); Cascata grande pr. Buriti, Malme 3474 (F); Buriti, Boca de Serra, Malme, Nov. 6, 1903 (US); Serra da Chapada, pr. Bocca de Serra, Malme 3474a (US); Serra da Chapada, Riedel 1057 (GH); Cuyaba, Schwacke 5006 (RB). ORINOCO: Esmeraldas, Luetzelburg 22491 (NY, R); Tamatama, Luetzelburg 22487 (UC). PARA: Serra de Paîtuna, Monte Alegre, Ducke (RB no. 21901) (RB). STATE UNKNOWN: Glaziou 388 (P); Glaziou 15788 (NY, UC); Riedel 29 (NY); Steere, in 1871 (MICH); Wright (NY); Tajung, coll. unknown (NY).

COLOMBIA. META: Villavicencio, near Río Guatiquia, Pennell 1544 (GH, NY, US). VAUPES: Río Kururu, Mesa de Yambi, savannah, Gooran-hoo-da, Schultes and Cabrera 19144 (US); San José del Guaviare, Río Guaviare, Cuatrecasas 7688 (F, US).

VENEZUELA. AMAZONAS: Esmeralda Ridge, between Esmeralda and base of Cerro Duida, Steyermark 57734 (GH, MO, NY, US); Esmeralda, Esmeralda Ridge, Tate 231 (NY, US).

Discussion. The dimorphic nature of A. buniifolia and A. millefolia has strongly affected their generic placement, Gardner having erected a separate genus for them and John Smith having transferred them to Mohria. As mentioned previously, I believe this character has been overemphasized, for it occurs independently in subg. Anemiorrhiza and many transitions have been found. Similarly, the extreme reduction in segment width has arisen independently in A. (subg. Anemia) tenera, a close relative of the common A. hirsuta in Brazil. A. buniifolia is most closely related to A. millefolia. A. buniifolia differs, however, in its orange rhizome hairs, its lack of marginal spicules, its subglabrous stipe, more lax appearance, anadromous pinnae, and smaller spores.

The two species grow together and have approximately the same geographical range, but there have been no collections of hybrids between the two.

8. Anemia millefolia Gardner ex Presl, Suppl. Tent. Pterid. 80. 1845. (Pl. XV, Fig. B).
Coptophyllum millefolium Gardner, London Jour. Bot. 1:133. 1842.
Mohria millefolia (Gardner) J. Smith, London Jour. Bot. 2:388. 1843.

Hemianemia millefolia (Gardner) Reed, Bol. Soc. Brot. II. 21: 158. 1948.

Rhizome horizontal, compact, up to 0.8 cm thick; hairs maroon; fronds caespitose, dimorphic; stipe of sterile frond terete, 1-8 cm long, nearly 1 mm thick, yellow to light brown, hirsute; blade oblong-ovate, tripinnate to quadripinnate; pinnae 6-12 pairs, catadromous, subsessile, pinnately divided; segments quite narrow, generally less than 0.5 mm broad, coriaceous; margin spiculate; fertile fronds taller than sterile, stipe 4-13 cm long; blade 2-8 cm long; pinnae subsessile, short, not spreading; spores 65-107 μ, tetrahedral-globose, the angle protuberances inconspicuous, the ridges smooth, solid.

Distribution. Interior Brazil, Venezuela, Colombia, and Panama (Pl. VIII, Fig. A).

Type collection. "In montosis aridis apud Villa de Arayas, prov. Goyazanae, [Brazil], Gardner 4083."

Specimens examined. BRAZIL. GOIAS: Chapada dos Veadeiros, 5 km w. of Veadeiros, Dawson 14712 (DAWSON); summit of a dry mountain range near Arrayas, Gardner 4083 (K, type; F, GH, NY); Gardner 4083B (NY); Goias, Morro S. Francisco, Macedo 3520 (NY, RB, US); Serra de Sta. Barbara, Ule 360 (GH, NY, UC); Serra dos Pyreneos, Ule 360 (RB); Burchell 7028 (GH). MATTO GROSSO: Cascata Grande, pr. Buriti, Malme 3473 (F, S-PA, US); Morro Podre, Hoehne 3833 (NY).

COLOMBIA. TOLIMA: Prado, Lehmann 6400 (K, US).

PANAMA. Coclé, vicinity of El Valle, Allen 1166 (MO, US).

VENEZUELA. BOLIVAR: Gran Sabana, in woods bordering stream tributary to Río Kukenán, at base of Mt. Roraima, Steyermark 58577 (F, MO, NY, US).

Discussion. Gardner says that this lacy species derives its name from its close resemblance of form to that of the yarrow, Achillea millefolium. Anemia millefolia has the widest geographical distribution of the species of sect. Coptophyllum, extending as far north as Panama.

9. Anemia rutifolia Martius, Ic. Crypt. Bras. 112. t. 55 f. 1. 1834 (Pl. XVI, Fig. A).

Anemia dimorphostachys Baker, Engl. Bot. Jahrb. 17:522. 1893.

Hemianemia dimorphostachys (Baker) Reed, Bol. Soc. Brot. II. 21:159. 1948.

Hemianemia rutaefolia (Martius) Reed, Bol. Soc. Brot. II. 21:159. 1948.

Rhizome horizontal, ca. 0.5 cm thick; hairs orange; fronds somewhat scattered; stipe terete, 1-21 cm long, 1 mm broad, yellow to light brown, subglabrous; blade deltoid-ovate, bipinnate to bipinnate-pinnatifid, coriaceous, 2-9 cm long; pinnae 5-11 pairs; pinnules slender, often as narrow as 1 mm, mostly anadromous, subglabrous on both surfaces; marginal spicules present; fertile pinnae 1-4 pairs, sessile, suberect, remote from the sterile pinnae, shorter than the sterile blade; spores 58-65 μ, tetrahedral-globose, the angle protuberances inconspicuous, the ridges smooth, solid.

Distribution. Minas Gerais, Brazil (Pl. VIII, Fig. A).

Type collection. "In asperis lapidosis Serra do Caraca, prov. Minarum [Brazil]." The type may be at BR, where the Martius herbarium is located.

Specimens examined. BRAZIL. MINAS GERAIS: Conselheiro Mata, Lama Preta, Brade 13946 (MICH, NY, US); Diamantina, Serra do Rio Grande, Mexia 5757 (F, MICH, MO, NY, UC, US); Grão Mogol, Markgraf, Barreto and Brade, no date (RB no. 39648) (RB); Serra do Caraça, Damazio in 1907 (RB no. 36907)(RB); Glaziou 20162 (BR, K, NY); Gardner 5339 (NY).

Discussion. Anemia rutifolia represents an intermediate step between the more generalized type of subg. Coptophyllum and the dissected, dimorphic A. millefolia and A. buniifolia. The number of pairs of fertile pinnae is variable, but never is the frond completely fertile. Furthermore, the laminar segments, though slender, are not as reduced as the more extreme forms.

10. Anemia glareosa Gardner in Field et Gardn., Sert. Pl. t. 70. 1844 (Pl. XVI, Fig. B).
Aneimia gardneriana Presl, Suppl. Tent. Pterid. 82. 1845.
Anemia oblongifolia var. microphylla Baker, Jour. Bot. 1885:218.
Hemianemia glareosa (Gardner) Reed, Bol. Soc. Brot. II. 21:160. 1948.

Rhizome horizontal, 0.5-0.7 mm thick; hairs orange; fronds caespitose; stipe terete, 1-11 cm long, 1 mm or less broad, dark brown, glabrous to pilose; blade oblong, simply pinnate to slightly pinnate-pinnatifid, chartaceous to coriaceous, subglabrous; pinnae 1-5 pairs, entire, crenate to pinnatifid; marginal spicules occasional; fertile pinnae petiolate, erect, remote to subapproximate to the sterile pinnae, exceeding the sterile blade; spores 78-87 μ, tetrahedral, the angle protuberances well developed, the ridges clear, solid.

Distribution. Goias, Brazil and southern Colombia (Pl. VIII, Fig. A).

Type collection. In dry gravelly places near Natividade, prov. Goyaz [Brazil], Gardner 4086.

Specimens examined. BRAZIL. GOIAS: Serra de Natividade, Gardner 4086 (K, type; BM, F, FI, G, P); Serra Santa Barbara, Ule 538 (R). RIO DE JANEIRO: Environs de Rio Janeiro et d'Ouro Preto, Damazio 15790 (K, NY); Burchell 659A (NY); Burchell 659A-2 (FI, GH, K). STATE UNKNOWN: Rocky Mountains, Creyer 107 (K).

COLOMBIA. TOLIMA & CAUCA: Patia Valley, near Bordo, White 18 (K). TOLIMA: Lehmann 6402 (P, US).

Discussion. Prantl places this species with A. gardneri and A. lanuginosa in sect. Gardnerianae on the basis of once pinnate dissection and coriaceous texture. He does not state the type of the section, but it is probably A. glareosa rather than A. gardneri, as Reed (1948) supposed. Anemia gardneriana is listed by Prantl as a synonym of A. glareosa.

It is placed in sect. Coptophyllum with some hesitation, for it shows no close relationship with the other three species of the section. There is no reduction of segment width nor is there any suggestion of sporangia being borne on pinnae other than the basal pair. The well-developed

spore angle protuberances are in contrast to those of the other three species. On the other hand, the small size of the plant, orange rhizome hairs, marginal spicules, floating stomates, and geographical range are features in common with the rest of the section.

D. Section Adetostoma

Section Adetostoma Mickel, sect. nov.

Rhizomatis apice horizontali et exposito aut ascendente atque petiolorum basibus vestito; pilis aurantiacis vel rubroaurantiacis; petiolo gracili (minus quam 1 mm lato); lamina bipinnata vel pinnata-pinnatifida, chartacea; cellulis epidermalibus cum bracchiis subquadratis; stomatibus liberis; pinnis fertilibus aut sessilibus aut brevipetiolatis, horizontalibus vel suberectis, remotis a pinnis sterilibus, brevioribus quam lamina sterili; sporae perinio levigato.

The species of this section resemble the generalized type of the subgenus in form and texture, but with a relatively primitive habit of the fertile pinnae and smaller size of the plant. The stomates are consistently floating, and it is on this character that the sectional name is based (Gr. adetos, free, and stoma, mouth or stomate).

Type species. Anemia brandegeea Davenport.

11. Anemia brandegeea Davenport, Fern Bull. 13:20. 1905 (Pl. XVII, Fig. A).
Hemianemia brandegeea (Davenport) Reed, Bol. Soc. Brot. II. 21:157. 1948.

Rhizome horizontal, ca. 0.4 cm thick; hairs orange; fronds caespitose; stipe terete, 1-2.5 cm long, less than 0.5 mm broad, yellow, hirsute; blade deltoid-ovate, pinnate-pinnatifid, chartaceous, 1.5-3 cm long; pinnae 3-5 pairs; pinna lobes rounded, hirsute on both surfaces; fertile pinnae sessile, horizontal, remote from the sterile pinnae; spores 61-75 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. Known only from the type collection (Pl. IX, Fig. B).

Type collection. Mexico, Sinaloa, vicinity of Culiacán, Cerro Colorado, on cliffs, T.S. Brandegee, 5 November 1904.

Specimens examined. MEXICO. SINALOA: Vicinity of Culiacán, Brandegee, in 1904 (GH, type; UC).

Discussion. The extremely small size of this plant is quite distinctive, but it is the only character I have found to separate it from A. intermedia. Other differences, such as degree of dissection, are probably only a reflection of the difference in size. Since each species is known from a single specimen, however, I hesitate combining the two until their variation is better known.

12. Anemia intermedia Copeland in M.E. Jones, Contrib. West. Bot. 15:123. 1929 (Pl. XVII, Fig. B).
Hemianemia intermedia (Copeland) Reed, Bol. Soc. Brot. II. 21:157. 1948.

Rhizome horizontal, less than 1 cm thick; hairs orange, fronds caespitose; stipe terete, 4-8 cm long, ca. 1 mm broad, light to dark brown, densely hirsute; blade deltoid-ovate, bipinnate to bipinnate-pinnatifid, chartaceous, 5-8 cm long; pinnae 7-10 pairs; pinnules narrowly adnate, oblong, crenate to pinnatifid, hirsute on both surfaces; fertile pinnae sessile, horizontal or slightly ascending, remote from the sterile pinnae, spores 56-81 μ, tetrahedral- lobose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. Known only from the type collection (Pl. IX, Fig. B).

Type collection. Mexico, Nayarit, Acaponeta, 'El Tigre Mine,' alt. 1000 m., M.E. Jones 23472, 1 March 1927. The holotype is with the Marcus E. Jones herbarium at POM.

Specimens examined. MEXICO. NAYARIT: Acaponeta, "Tiger Mine," Jones 23472 (UC, isotype).

Discussion. Anemia intermedia is intermediate between A. brandegeea and A. smithii in its size, the medium brown stipe color, and slightly ascending fertile pinnae. If the three species are distinct, A. intermedia may either represent an intermediate stage in the divergent evolution of the group or be of hybrid origin from the other two species.

13. Anemia smithii Brade, Bol. Mus. Nac. Rio de Janeiro, 5(3):95. t. 3. 1929 (Pl. XVIII, Fig. A).
Hemianemia smithii (Brade) Reed, Bol. Soc. Brot. II. 21:157. 1948.

Rhizome apex ascending and clothed with petiole bases; up to 0.7 cm thick; hairs orange; fronds caespitose; stipe terete, 2-15 cm long, less than 1 mm broad, medium to dark brown, hirsute; blade elongate-deltoid, bipinnate, chartaceous, 4-13 cm long; pinnae 5-11 pairs; pinnules oblong, broadly adnate, entire to crenate, pilose on both surfaces; fertile pinnae short-petioled, suberect, remote from the sterile pinnae, not exceeding the sterile blade; spores 81-97 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. From western Brazil along the Andes to Panama (Pl. IX, Fig. B).

Type collection. "In Braziliae statu Mato Grosso, Herbert Smith 132 ex parte, 1886." According to Brade, the type is at R.

Specimens examined. COLOMBIA. META: Río Duda, Fosberg 19475 (US).

PANAMA. Chiriqui, trail from San Felix to Cerro Flor, Allen 1925 (GH, MO, US).

PERU. JUNIN: e. of Quimiri Bridge, near La Merced, Killip & Smith 23951 (NY, US); Colonia Perene, Killip & Smith 25036 (NY, US); along the Perene, near Hacienda 3, Colonia Perene, Killip & A.C. Smith 25194 (F, NY, US); Chanchamayo Valley, Schunke 78 (F, US); Schunke Hacienda, above San Ramón, Schunke A137 (US).

BOLIVIA: LA PAZ: Pata, Williams 2584 (GH, NY, US), Williams 2586 (NY, US).

Discussion. In its dissection, oblique rhizome, and hirsute stipe, this species looks very much like a small specimen of A. flexuosa, which has approximately the same geographical range. However, it probably has no direct relationship with A. flexuosa. Its characters of size, stipe,

floating stomates, fertile pinnae, and spores tie it more closely to A. brandegeea and A. intermedia. The species is apparently uncommon, but with a wide geographical distribution.

E. Section Trochopteris

Anemia subg. Coptophyllum sect. Trochopteris (Gardner) Mickel, stat. nov.
Trochopteris Gardner, London Jour. Bot. 1:74. 1842.
Anemia subg. Trochopteris (Gardner) Sturm in Mart., Fl. Bras. 1(2): 187. 1859.
Hemianemia subg. Trochopteris (Gardner) Reed, Bol. Soc. Brot. II. 21:156. 1948.

Plants small, the sterile fronds less than 10 cm long; rhizome oblique or erect; fronds forming a flat rosette; blade pinnatifid to pinnate-pinnatifid, chartaceous, tomentose to lanose; epidermal cells with sinuous arms; spore perine smooth.

Type species: Anemia elegans (Gardner) Presl.

14. Anemia elegans (Gardner) Presl, Suppl. Tent. Pterid. 81. 1845 (Pl. XVIII, Fig. B).
Trochopteris elegans Gardner, London Jour. Bot. 1:74. t.4. 1842.
Hemianemia elegans (Gardner) Reed, Bol. Soc. Brot. II. 21:156. 1948.

Rhizome oblique or erect, inconspicuous; hairs orange; fronds forming a flat rosette; fronds usually nearly sessile, up to 2 cm long, obovate, pinnatifid; lobes 3-5, rounded, chartaceous, tomentose on both surfaces, the stomata located in the upper epidermis; sporangia borne on the basal lobes of the frond; spores 65-75 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. Goias and Minas Gerais, Brazil (Pl. IX, Fig. B).

Type collection. "In fissuris rupium quartzoso-schistosarum in summo monte Serra de Natividade, Provincia Goyazanae Braziliae, ubi copiose inveni mense Februari, 1840, Gardner 4085." The type is probably at K, where the Gardner collections are located.

Specimens examined. BRAZIL. GOIAS: Serra de Natividade, Gardner 4085 (NY, isotype). MINAS GERAIS: Diamantina, Brade 13951 (RB), Glaziou 20163 (NY, UC, US), Damazio 1825 (DEN), Damazio 1875 (NY, S-PA, UC, US); Itacolomy, Damazio, in 1903 (RB no. 36906) (RB); Serra do Itacolomy, Gomes 942 (MICH); Ouro Preto, Itacolmi, Macedo 2805 (US); Ouro Preto, Maublanc 652 (F), Maublanc 653 (F); Paruna, Schwacke 8020 (RB); Serra do Cipó, 110 km northeast of Bello Horizonte, Chase 9219½ (US); Serra da Lapa, Riedel 6037 (NY); Baipendi, São Thomé das Letras, Brade 20416 and Apparicio (MICH); Glaziou, no date (NY).

"CUBA" [?]: Linden 1906 (RB).

Discussion. The great botanist Goebel (1915) concluded that the simple form of A. elegans is probably a reduced condition, perhaps a case of neotony. Although this species certainly shows a specialized condition, the case for neotony is weakened by the intermediate form found in A. eximia.

The unusual habit of this plant brought Gardner (1842a) to describe a new genus for it, but in spite of its striking appearance, most of its characters tie it closely to subg. Coptophyllum. Many of the distinctive features of this plant reflect its small size: slight dissection, sporangia borne on lobes, rhizome nearly absent. The conspicuous hairs of the plant are different from those of most other species of the subgenus, however, in being composed usually of only one cell and lacking a glandular tip cell. This type of hair is found occasionally in A. eximia and is the dominant hair type on the adaxial leaf surface in A. colimensis.

15. Anemia eximia Taubert, Engl. Jahrb. 21:422. 1896 (Pl. XIX, Fig. A).
Anemia schwackeana Christ, Farnkr. 351. 1897.
Hemianemia eximia (Taubert) Reed, Bol. Soc. Brot. II. 21:156. 1948.

Rhizome short, ascending or erect, inconspicuous; hairs maroon; fronds forming a flat rosette; stipe terete, up to 3 cm long, 2.0-2.5 mm broad, yellow, villous; blade ovate, pinnate to pinnate-pinnatifid, chartaceous, up to 5.5 cm long; pinnae 4-5 pairs, entire, lobes rounded, villous; fertile pinnae sessile, horizontal, remote from the sterile pinnae, about as long as the lowest sterile pinnae; spores 65-75 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. Goias, Brazil (Pl. IX, Fig. B).

Type collection. "In rupibus montium Serra dos Pyreneos, Ule 3208." I have seen a photograph of the type which is at P.

Specimens examined. BRAZIL. GOIAS: Serra Dourada, Ule 540 (P, R); Glaziou 22626 (BR, G, RB p.p.).

Discussion. Anemia eximia provides an intermediate step between A. elegans and the more generalized form of subg. Coptophyllum, as shown by its size, dissection, and details of its anatomy. The epidermal cells are not as extremely contorted as in A. elegans, and the laminar hairs are usually composed of two or more cells, in contrast to the large unicellular hairs of A. elegans.

Relationships to other sections of subg. Coptophyllum are not clear. It is probable that the simple form of A. elegans is secondarily derived. A relationship with the A. villosa group of species has been postulated on the basis of the common characters of simply pinnate plan, chartaceous texture, and spore ridges lacking a medulla. On the other hand, affinity to A. trichorrhiza is possible, as is mentioned above.

F. Section Tomentosae

Aneimia subg. Hemianeimia sect. Tomentosae Prantl, Schiz. 87. 1881.
Hemianemia subg. Eu-Hemianemia sect. Tomentosae (Prantl) Reed, Bol. Soc. Brot. II. 21:160. 1948.

Fronds erect and spreading, generally 20-60 cm long; stipe terete, rarely flattened; fertile pinnae petiolate and erect; spore ridges usually containing a spongy medulla; perine smooth.

Type species. Anemia tomentosa (Savigny) Swartz.

The section Tomentosae includes 23 species, which will be treated in approximately the order found on the chart of relationships (Pl. XI).

16. Anemia sessilis (Jeanpert) C. Chr., Fedde Repert. Sp. Nov. 9:371. 1911.
Anemia tomentosa var. sessilis Jeanpert, Bull. Mus. Hist. Nat. 1910:403. 1910.
Hemianemia sessilis (Jeanpert) Reed, Bol. Soc. Brot. II. 21:157. 1948.

Rhizome horizontal, up to 1 cm thick; hairs maroon; fronds caespitose; stipe terete, 2.5-10 cm long, less than 1 mm broad, yellow to light brown, hirsute; blade deltoid-ovate, deeply pinnate-pinnatifid to bipinnate, chartaceous, 5-8 cm long; pinnae 5-7 pairs; segments broadly adnate, rounded, pilose; fertile pinnae petiolate horizontal to suberect, remote from the sterile pinnae, shorter than the sterile blade; spores 62-72 μ, globose, the angles rounded, the ridges smooth, spongy-medullate.

Distribution. French Guinea, northern Nigeria, and Ruanda Urundi, French Equatorial Africa (Pl. VII, Fig. B).

Type collection. "Guinee Francaise, Vallei de los Kakrimos, Koussi, Jan. 1910, H. Pobeguin (15) 2234." The type is reported by Jeanpert to be in the Bonaparte herbarium, which is at P.

Specimens examined. FRENCH GUINEA. Vallei de les Kakrimos, Koussi, Pobeguin (15) 2234 (P, isotype); Rouria, Nickles, no date (BR).

FRENCH WEST AFRICA. Ht. Dahomey, Mt. Atacora, pays Samba, Chevalier 24164 (BR, P).

NORTHERN NIGERIA. Uru, Rauchi Plateau, Dent Young 265 (K); Naraguta, Lely 307 (K).

Discussion. Anemia sessilis is poorly represented in herbaria. It appears to be a relatively primitive species on the basis of its horizontal to suberect fertile pinnae and maroon rhizome hairs. These characters in addition to its small size make this species a rather distinctive one in comparison to the other African members of the section.

Specimens similar to the above description in many respects from Nigeria and French Equatorial Africa may represent a distinct variety or species (Pl. XIX, Fig. B). Their spores are tetrahedral-globose and larger (82-91 μ) with angle protuberances and not such a granular appearance of the spongy medulla in the spore ridges. They also seem to have a heavier texture. The species has been characterized by the small size of all the specimens and the horizontal to suberect habit of the fertile pinnae. Further collections are necessary in order properly to evaluate the variation patterns within this species.

17. Anemia madagascariensis C. Chr., Arch. Bot. (Caen) Bull. mens. 2:216. 1928 (Pl. XX, Fig. A).
Hemianemia madagascariensis (C. Chr.) Reed, Bol. Soc. Brot. II. 21:162. 1948.

Rhizome horizontal, ca. 1 cm thick; hairs reddish-orange; fronds caespitose; stipe terete, 10-16 cm long, ca. 1 mm broad, yellow to light brown, hirsute; blade deltoid-ovate, bipinnate-pinnatifid to tripinnate, chartaceous, 8-10 cm long, densely hairy on the rachis, costae and veins; pinnae 7-19 pairs; segments narrowly adnate, obovate, entire; fertile

Cockburn 60 (BM); Perrottet 1408 (BM, F, P); Lobb, no date (P); Johnston 26 (K); Beddome 164 (K); Gardner and Wight, Nov. 1846 (BM); Gardner, no date (K, type); Gardner, no date (BM). DISTRICT UNKNOWN: Wight 3181 (GH); Gouche 57 (BM); Herb. Limming (FI).

MALAYA [?]. Lobb 39 (MO).

Discussion. Although Anemia wightiana has often been treated as A. schimperiana, it is quite distinct from it. It resembles A. schimperiana in dissection, but A. wightiana is much more hairy, the rhizome apex is ascending and covered with petiole bases, and the stipe is stouter; the spores are considerably larger and have conspicuous angle protuberances.

Its isolated geographical position in relation to the rest of the genus is probably a remnant of a much broader range in the past.

21. Anemia simii Tardieu, Notul. Syst. 14:208. 1951 (Pl. XXII, Fig. A).

Rhizome horizontal, 0.5-1.0 cm thick; hairs orange; fronds caespitose; stipe terete, 8-30 cm long, ca. 1 mm broad, yellow, subglabrous to pilose; blade deltoid, bipinnate to deeply bipinnate-pinnatifid, chartaceous to subcoriaceous, 6-15 cm long; pinnae 6-13 pairs; pinnules narrowly adnate, oblong-ovate, entire; lobes oblong, pilose; fertile pinnae petiolate, erect, approximate to the sterile pinnae, greatly exceeding the sterile blade, glabrous; spores 78-99 μ, tetrahedral-globose, the angle protuberances conspicuous, ridges smooth, spongy-medullate.

Distribution. South Africa, Southern Rhodesia, and Mozambique (Pl. VII, Fig. B).

Type collection. Transvaal Barberton, Thorncroft 959. I have not seen the type, but it is presumably at P, where Mme. Tardieu-Blot is a sub-director. The paratype of A. simii (Angola, Cascade du Cutato, Rohan Chabot) belongs to A. angolensis, which had not been described at the time of Tardieu's publication.

Specimens examined. MOZAMBIQUE. Manica e Sofala: Manica, Mavita, estrada, Macequece, Barbosa 1403 (BM); Melsetta Rhodesi, Johnson 180 (K).

SOUTH AFRICA. Transvaal, Barberton, Thorncroft XI (P); Transvaal, P. K. Ellieras Spruitskloof, Waterberg, Therou, in 1956 (PRU no. 11152) (BM); Natal, Lisepopo, Sanderson, in 1871 (K); Natal, 20 mi. from Umbali on Bura Rd., Fisher 1292 (BM).

SOUTHERN RHODESIA. Belingive East Reserve, Wild 43603 (BM); Umtali, Hondi River, Chase 3290 (BM); Umtali, Meneni River, Chase 3313 (BM); Border Post, Umtali, Meneni River, Fischer and Schweickerdt 432 (BM, BR, MO); Chibi, 10 mi. n.e. of Lundi River bridge, Schelpe 4088 (BM, US); Mazoe Dam, Guilliland B197 (BM); Nyumquarara, Guilliland 1646 (BM); Makoni, Forest Hill Kop, Eyles 726 (K); Peter 30927 (UC).

Discussion. Of the eight African species of sect. Tomentosae, A. simii bears the closest resemblance to the widespread variable New World species, A. tomentosa. Although the dissection and rhizome hair color are quite similar, they differ in the segments being much more slender and pointed (ca. $\frac{1}{3}$ as broad as long versus more than $\frac{1}{2}$ as broad as long), and in details of spore and leaf morphology.

22. Anemia angolensis Alson, Estud., Ens. e Doc. Min. do Ultramar [Lisboa] 12 (Contrib. Fl. Mocambique 2): 9 t. 2, 3a. 1954 (Pl. XXII, Fig. B).
Anemia schimperiana var. angustiloba Bonaparte, Not. Pterid. 1:133. 1915.
Hemianemia schimperiana var. angustiloba (Bonaparte) Reed, Bol. Soc. Brot. II. 21:162. 1948.
Anemia simii var. angustiloba (Bonaparte) Pichi-Sermolli, Webbia 9:654. 1954.

Rhizome horizontal, 0.8-1.5 cm thick; hairs maroon; fronds caespitose; stipe terete, 5-10 cm long, 1-2 mm broad, yellow, pilose; blade deltoid-ovate, bipinnate to bipinnate-pinnatifid, subcoriaceous, 7-16 cm long; pinnae 6-14 pairs; pinnules oblong-ovate, narrowly adnate, lobed to pinnatifid; lobes usually obtuse, pilose; fertile pinnae petiolate, erect, approximate to the sterile pinnae, exceeding the sterile blade, densely and finely pubescent; spores 88-101 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, spongy-medullate.

Distribution. Angola, southern Belgian Congo, Northern Rhodesia, and Tanganyika (Pl. VII, Fig. B).

Type collection. "Angola, Huila entre rochedos, 5600 ft., Morro de Monhino, Welwitsch 164." Alston reports that the type is at BM.

Specimens examined. ANGOLA. Cascades du Cutalo, Rohan Chabot, 23 Jan 1913 (BR, K, UC); Langdingo, Kaconda, Gossweiler 4283 (BM); Planalto de Benguela, Babaera, Cuiva-Catumbela, Gossweiler 9705 (K, US); Huilla, Morro de Monino, Serra de Neve, Welwitsch 164 (K, isotype); Huilla, Autimies, no date (BR).

BELGIAN CONGO. Katanga, Kafubu, Dom Bosco, Guarré 262 (GH, BR); Lubemba Valley, Kassner 2389 (BM, K); Elizabethville, Shantz 511 (US); Station de Keyberg, 8 km. southwest of Elizabethville, Schmitz 100 (BR); Lukafu, contrefort des Kundelunger, Schmitz 1775 (BR); Parc National de l'Upemba, Kabwoe, Kiluba Shindikila, coll. illeg. 03820 (BR); Parc National de l'Upemba, Karunga, Vallei de Co. in Lubanga, coll. illeg. 05609 (BR); coll. illeg. 05631 (BR).

NORTHERN RHODESIA. Kalambo Falls, Richards 1244 (US); Lake Tanganika, Kalambo Falls, pres d'Abercorn, coll. illeg. 1368 (BR); Kalenda Ridge, west of Matonchi Farm, Mwinilunga District, Milne-Redhead 4267 (BM, BR); Northern Prov., Kalambo Falls, Exell, Mendonça & Wild 1272 (BM); 6 miles east of Lusaka, King 271 (K); Mumbwa, Macaulay 1047 (K).

NYASALAND. Langenburg, Rumbiza-Thal, Goetze 831 (BR); Northern Province, Njakwa Gorge, Chapman 252 (BM).

SOUTHERN RHODESIA. Urungwe, Mopane-Mfuti, 11 miles north of R. Mauora, Phipps 956 (BR).

TANGANYIKA. Miverasi, coll. illeg. 1495 (BR); Mahenge, Mbangala, Schlieben 1775 (BR, S-PA).

COUNTRY UNKNOWN. Chilla, Newlin 11 (K).

Discussion. This species closely resembles A. simii in the eastern part of its range and has often been confused with it. What has been called A. simii var. angustiloba was collected in Tanganyika. I have seen a photograph of this plant, and on the basis of its locality and its

apparent similarity to the specimens of A. angolensis from that region, I would place it with the latter. I believe our knowledge of the African species of Anemia is too scanty to designate the specimens of Northern Rhodesia and Tanganyika as a variety.

Anemia angolensis can be distinguished from A. simii by the maroon rhizome hairs, stout stipe, densly pubescent fertile pinnae, and usually broader segments of A. angolensis. The two species are closely related.

23. Anemia nigerica Alston, Bol. Soc. Brot. II. 30:6. 1956.

Rhizome ascending, 1.0-2.5 cm thick; hairs reddish-orange; fronds caespitose; stipe terete, yellow, 11-30 cm long, 2-3 mm broad, hirsute to villous; blade deltoid-ovate, bipinnate-pinnatifid, chartaceous, 15-26 cm long; pinnae 1-13 pairs; pinnules oblong-ovate; broadly adnate, pilose; lobes obtuse; fertile pinnae petiolate, erect, approximate to the sterile pinnae, slightly exceeding the sterile blade; spores 85-111 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, spongy-medullate.

Distribution. Southern Nigeria (Pl. VII, Fig. B).

Type collection. Ondo Province, Ondo District: Carter Peak, Idanre Hills, on rocky slopes in forest of Hymenodictyon floribundum, Keay and Onochie FHI 21562. Dr. Dandy, Keeper of Botany at BM, reports that the type is in that herbarium (personal communication).

Specimens examined. NIGERIA. Ondo Province, Akure, Idanre: Carter Peak, Keay FHI 22653 (BM); Keay FHI 22725 (BM); Richards 3736 (BM).

Discussion. The most noteworthy feature of this species is its large size. As Alston points out, A. nigerica most closely resembles A. schimperiana. Similarities are especially strong in rhizome hair color, blade dissection and texture, and flattened rachis.

24. Anemia villosa Humb. and Bonpl. ex Willd., Sp. Pl. 5:92. 1810. (Pl. XXII, Fig. A).
Anemia obtusa Desv., Ges. natfdr. Frde. Berlin, Mag. 5:308. 1811.
Osmunda villosa Poir., Enc. Suppl. 4:231. 1816.
Aneimia ferruginea α minor Presl, Rel. Hänk 1:75. 1825.
Aneimia villosa γ humboldtiana Presl, Suppl. Tent. Pterid. 83. 1845.
Aneimia oblonga Sturm in Mart., Fl. Bras. 1(2):206. 1859.
Aneimia flexuosa β oblonga Prantl, Schiz. 94. 1881.
Aneimia flexuosa γ villosa Prantl, Schiz. 95. 1881.
Aneimia tomentosa var. oblonga (Sturm) Farwell, Am. Midl. Nat. 12:307. 1931.
Anemia tomentosa var. oblonga (Sturm) Reed, Bol. Soc. Brot. II. 21:161. 1948.
Hemianemia villosa (Humb. and Bonpl. ex Willd.) Reed, Bol. Soc. Brot. II. 21:162. 1948.

Rhizome apex horizontal and exposed or ascending and clothed with petiole bases, 1-2 cm thick; hairs maroon or orange; fronds caespitose; stipe terete, occasionally flattened at the base, 3-33 cm long, 1-2 mm broad, yellow to light brown, rarely drying to dark brown, villous to

hirsute; blade linear-oblong, pinnate-pinnatifid, chartaceous to subcoriaceous, 5-26 cm long; pinnae 7-19 pairs, shallowly to deeply incised but rarely to the costa; lobes rounded, 3-5 pairs per pinnae, hirsute to villous; fertile pinnae petiolate, erect, remote or approximate to the sterile pinnae, shorter or longer than the sterile blade; spores 81-108 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. In eastern Brazil from Santa Catarina north to Ceará and in northern South America from Peru to Surinam (Pl. VIII, Fig. B).

Type collection. I have not seen the type. The type locality is described only as "America meridionale," but there can be no question as to its identity. The term in the type description "fronde bipinnatifida oblonga" can refer only to this species. The other species of Anemia in northern South America are quite distinct. Since the type is not in the Humboldt herbarium at P (C.V. Morton, personal communication), it is probably in the Willdenow herbarium at Berlin.

Selected specimens examined. BRAZIL. BAHIA: Casa de Pedra, Luetzelburg 249 (NY, S-PA, UC). CEARA: Ibeapaba, Capanema, no date (RB no. 6706) (RB). ESPIRITO SANTO: Sta. Maria, Brade 18367 (RB). MINAS GERAIS: Distrito Diamantina, Barão, 1 km. along railroad, Mexia 5891 (F, G, GH, MICH p.p., MO, NY, R, UC, US). PARANA: Serra do Mar, Cadeado, Dusen 8304 (BM, G, GH, K, MO, NY, S-PA, US). PERNAMBUCO: Eng. Pelada, Quipapá, Leal & da Silva 240 (G, NY, RB). RIO DE JANEIRO: vicinity of Monte Serrat, Mt. Itatiaya, Estacão Biologica, L.B. Smith 1592 (BM, F, GH, NY, UC, US). SANTA CATARINA: Itajaí, Morro do Baú, Rietz 2049 (RB, HBR, US). SAO PAULO: Alto Bôa Vista, Brade 8584 (NY, UC).

BRITISH GUIANA. Mt. Roraima, Kanuku Mountain, Quelch & McConnell 272 (K); Mt. Roraima, Philipp Camp, Tate 317 (NY, US).

COLOMBIA. ANTIOQUIA: Sta. Elena, near Medellín, Daniels 158 (F, NY). BOGOTA: Gachalá, Linden [?] 211 (FI). BOYACA: Sierra Nevada de Cocuy, around Báchira, Grubb & Guymer 70 (US). CAUCA: Cauca Valley, Cuatro Esquinas, Pennell & Killip 6317 (GH, NY, US). CUNDINAMARCA: Caqueza to Río Sananie, Pennell 1340 (GH, NY, US). HUILA: Soma de San Antonio, inter San Luis et Río Chiquilá, Woronow 7150 (US). MAGDALENA: Santa Marta, Campo Alegre, H.H. Smith 1107 (BM, F, GH, MO, NY, S-PA, US). NORTE DE SANTANDER: Ocaña, Schlim 652 (BR, FI, G). SANTANDER: Eastern Cordillera, northern slope of Mesa de los Santos, Killip & A.C. Smith 15011 (BM, GH, NY, US). TOLIMA: Mt. Tolima, Tracey 222 (K). VALLE DEL CAUCA: Cerro de las Cruces, near Cali, western Cordillera, Killip & Cuatrecasas 38413 (F).

ECUADOR. Encima de Zaruma, Espinosa E1763 (NY); in mont. cerca Loxa, Hartweg 860 (BM); Chimborazo, André 865 (K).

PERU. SAN MARTIN: in monte Campana prope Tarapoto, Spruce 4708 (BM, BR, G, NY, US).

VENEZUELA. ARAGUA: Colonia Tovar, Fendler 6 (BM, BR, G, GH, K, MO, US). BOLIVAR: Mt. Roraima, Glycon Swamp and vicinity, southwest-facing slopes, Steyermark 58632 (MO, NY, US). CARABOBO: Carabobo, Montalboa, Funck & Schlim 691 (BM, BR). DISTRITO FEDERAL: between Cotiza and Los Venados, near Caracas, Allart 10 (NY, US). MERIDA: Páramo de Chacanta, Jahn 903 (US). MIRANDA: hills above Los Teques, Pittier 11596 (NY, US).

Discussion. Anemia villosa is the most abundantly collected species of subg. Coptophyllum. Although most specimens of the species are distinctive with their elongate form and pinnate-pinnatifid dissection, there is considerable variation in size and form that can lead to confusion with other species.

Amid the great variation within A. villosa, there can be pointed out certain morphological tendencies, which are correlcted with geographical range. With more intensive study of local variation these "tendencies" may prove to be varieties of this complex species.

Specimens from northern South America, from Peru to the states of Ceará and Pernambuco in Brazil, are relatively uniform and are characterized by their horizontal rhizome clothed with maroon or red hairs and the origin of the fertile pinnae at some distance from the sterile pinnae.

Of the abundant material from central Brazil the specimens most closely resembling these have been collected in the general area of the state of Minas Gerais. The rhizomes are horizontal and bear maroon hairs, but they differ in the position of the fertile pinnae being approximate or subapproximate to the sterile pinnae. Such plants are found in Minas Gerais, adjoining portions of São Paulo, and a few in Rio de Janeiro.

In Rio de Janeiro most of the specimens have oblique rhizomes, the rhizome apex ascending and covered with petiole bases. The rhizome hairs are orange. These specimens fall into two classes. The larger of the two groups consists of specimens with the typical linear form and with fertile pinnae approximate to the sterile pinnae. Some of these are extremely slender, and Sturm distinguished them as a separate species, Anemia oblonga. This has usually been treated as a variety or a synonym of A. villosa.

The other group of specimens in Rio de Janeiro are broader with fertile pinnae varying in their origin from remote to approximate to the sterile pinnae. In their outward appearance this group grades into A. raddiana. On the basis of the oblique rhizome habit and the orange rhizome hairs, I have placed it with A. villosa, but I am unable to find additional characters with which to distinguish the two species. This is probably a case of convergent evolution of form since on the basis of other characters I am certain the broad form of A. villosa and apparently similar specimens of A. raddiana are derived from unrelated types. I do not know whether the broad specimens of A. villosa represent an ecological form or a genetically fixed variation of that species.

A fifth "tendency" within the species is found in the more southern Brazilian states of Paraná and Santa Catarina. The pinnae are shallowly incised (less than halfway to the costa), the lobes being quite round and few (3-5 per pinna). The fertile pinnae are remote from the sterile pinnae. Both stipe and lamina are clothed with black hairs in contrast to the typical orange hairs of the other forms of A. villosa and most other species.

In Brazil there are a number of otherwise normal specimens which have abortive spores. An explanation for this condition lies in the probability of a polyploid series within A. villosa. On the basis of spore and stomatal sizes, A. villosa is probably a polyploid species, but many

specimens in Minas Gerais and Rio de Janeiro are probably higher polyploids. Hybridization between plants of the two genomic levels could well produce sterile plants.

Putative hybrids have also been found between A. villosa and four other species: A. organensis, A. imbricata, A. raddiana, and A. ferruginea. Extensive field work in Brazil is necessary to study properly the ecological variation, cytology, and inter- and infra-specific action.

25. Anemia organensis Rosenstock, Fedde Repert. Sp. Nov. 20:95. 1924 (Pl. XXIII, Fig. B).

Rhizome oblique, the apex covered with petiole bases, 0.8-1.5 cm thick; hairs orange; fronds caespitose; stipe terete, flattened at the base, 14-70 cm long, 1-2 mm broad, yellow to dark brown, pilose; blade linear-lanceolate, once pinnate, chartaceous, 16-45 cm long; pinnae 12-22 pairs, oblong, entire to crenate, pilose to hirsute; fertile pinnae petiolate, erect, remote to subapproximate to the sterile pinnae, approximately the same length as the sterile blade; spores 78-88 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. Rio de Janeiro and Espírito Santo, Brazil (Pl. VIII, Fig. B).

Type collection. Two specimens are cited by Rosenstock with his description of the species: "Rio de Janeiro, Serra Estrella, Costa Gamma, 1912, Luetzelburg 12962; Orgelgebirge, Morro Retiro, Oktober 1916, Luetzelburg 9933." Because of irregular numbering of the one (Luetzelburg 9933 & 6933), I am designating Luetzelburg 12962 as the lectotype. The Rosenstock Herbarium is located at S-PA.

Specimens examined. BRAZIL. ESPIRITO SANTO: Alto Limoeiro, Brade 18210 (MICH, NY). RIO DE JANEIRO: Frade de Macahé, Brade 15817 (NY, RB); Petrópolis, Araras, Spannagel 543 (NY, R, S-PA, UC), Spannagel 543c (NY, UC); near Petrópolis, Ball, 10-16 July 1862 (GH, US); Sta. Maria Magdalena, Sto. Antonio do Imbé, prope da Villa Imbé, Brade & Santos Lima 11650 (R), Brade & Santos Lima (H. P. no. 31102) (BM); Sta. Maria Magdalena, Santos Lima 153 (RB); Organ Mts., Rose 20800 (NY, US); Serra dos Orgãos, Morro Retiro, Luetzelburg 9933 (MICH, UC), as 6933 (NY, UC); Serra Estrella, Costa Gama, Luetzelburg 12962 (S-PA, isolectotype); Lenfman, in May 1872 (K).

Discussion. Anemia organensis is probably derived from the "oblonga" element of A. villosa, which it resembles in rhizome habit and hair color, and in laminar texture.

26. Anemia imbricata Sturm in Mart., Fl. Bras. 1(2):205. 1958. (Pl. XXIV, Fig. A).

Rhizome horizontal, 1-3 cm thick; hairs maroon; fronds caespitose; stipe terete, occasionally flattened at base, 8-25 cm long, 2-3 mm broad, yellow to dark brown, tomentose to villous; blade deltoid-ovate, pinnate-pinnatifid to nearly bipinnate, 8-18 cm long, coriaceous, usually drying to brown or nearly black; pinnae 9-18 pairs; lobes 5-6 per pinna, ovate-obtuse to oblong, tomentose to subglabrous; fertile pinnae petiolate, erect, subremote to subapproximate to the sterile pinnae, equal to or

pinnae petiolate, erect, remote from the sterile pinnae, shorter than the sterile blade; spores 97-104 μ, tetrahedral-globose, the angles rounded, the ridges smooth, spongy-medullate.

Distribution. Madagascar (Pl. VII, Fig. B).

Type collection. "Plateaux et vallées de l'Isalo, gorges de la Sakamerekely et de la Sambalinieto, grès et sables siliceus, Humbert 2857." I have seen a photograph of the type, which is in the Christensen herbarium at BM.

Specimens examined. MADAGASCAR. Plateaux et vallées de l'Isalo, Humbert 2857 (GH, P, isotypes).

Discussion. This rare species is very distinct in its fine dissection and dense hairs. It has no clear relationships with any other species.

18. Anemia schimperiana Presl, Suppl. Tent. Pterid. 84. 1845. (Pl. XX, Fig. B).
Anemia tomentosa β schimperiana (Presl) Moore, Ind. Fil. 70. 1857.
Hemianemia schimperiana (Presl) Reed, Bol. Soc. Brot. II. 21:162. 1948.

Rhizomes horizontal, up to 1 cm thick; hairs orange; fronds caespitose; stipe terete, occasionally slightly flattened near the blade, 4-5 cm long, 1-1.5 mm broad, yellow to light brown, pilose to hirsute; blade deltoid-ovate, bipinnate to bipinnate-pinnatifid, chartaceous, 6-13 cm long; pinnae 7-9 pairs; pinnules broadly adnate, ovate to oblong-ovate, pilose; fertile pinnae petiolate, erect, remote to subapproximate to the sterile pinnae, shorter than to only slightly exceeding the sterile blade; spores 78-91 μ, tetrahedral-globose, the angle protuberances short to lacking, the ridges smooth, spongy-medullate.

Distribution. Ethiopia and Eritrea (Pl. VII, Fig. B).

Type collection. "Abyssinia, in regione Gafta, 14 Sept. 1838, Schimper 1203." The type is reported by Pichi-Sermolli (1954a) to be in the Presl herbarium at PRC. Although the holotype was not seen, the many isotypes agree with the description and are quite uniform except for a supposed isotype at MO. Quite likely an error was made in the mounting process, the label being affixed to the wrong specimen. From all the morphological features examined the MO specimen seems to be A. raddiana of Brazil.

Specimens examined. ERITREA. Hamasen, Ghinda in val Baresa, Fiori 819 (FI).

ETHIOPIA. Bodessa, Mearns 108 (BM, US); Gafta, Schimper 1203 (BM, BR, FI, G, GH, K, P, S-PA, UC, isotypes); slopes of the Mugur Valley, 30 mi. n. of Addis Ababa, Sandford 9 (BM); Quartin-Dillon and Petit, in 1844 (P); no data (F).

Discussion. Anemia schimperiana was the first species of the subgenus to be described from Africa. The rounded pinnules are characteristic for this species and for a few other of the Old World species. On this basis A. sessilis, A. wightiana, A. nigerica, and A. aethiopica show a relationship. Anemia schimperiana is probably most closely related to A. aethiopica in spite of the latter's great specialization in several characters, the most striking being its flattened stipe and its spores with anastomosing ridges. Occasional specimens of A. schim-

periana have shown suggestions of both of these characters. The two species also share such characters as the orange rhizome hairs, fertile pinnae subapproximate to the sterile, and fairly small spore and stomate size.

19. Anemia aethiopica Pichi-Sermolli, Webbia 9:654 Fig. 5. 1954 (Pl. XXI, Fig. A).

Rhizome horizontal, ca. 1 cm thick; hairs orange; fronds caespitose; stipe flattened, 7-12 cm long, ca. 2 mm broad, yellow, tomentose; blade oblong-deltoid, bipinnate to bipinnate-pinnatifid, chartaceous, 11-14 cm long; pinnae 8-9 pairs; pinnules broadly adnate, oblong, lobed, pilose; fertile pinnae petiolate, erect, subremote from the sterile pinnae, longer than the sterile blade; spores 75-88 μ, tetrahedral-globose, the angles rounded, the ridges smooth, spongy-medullate, freely anastomosing.

Distribution. Southeastern Ethiopia (Pl. VII, Fig. B).

Type collection. "Somalia, Paese dei Gherire, Zona tra El Marà e Monte Ellot, 8 Nov. - 2 Dic. 1937, riscontrata presso El Marà nei luoghi più umidi e come sottobosco prevalente del Bosso, Reghini 2." I have not seen the type, but it is reported by Pichi-Sermolli to be at FI.

Specimens examined. ABYSSINIA. Western Sidano Forests, Brockman 171 (K).

Discussion. The only specimen I have seen of this species, a paratype, closely fits the type description: the flattened stipe and rachis, bipinnate-pinnatifid dissection, fertile spikes longer than the sterile blade, equal distances between pinnae, heavy indument of stipe and rachis, and spores with anastomosing ridges. Pichi-Sermolli describes the ridges as being irregular, occasionally anastomosing. I find tham to be regularly anastomosing in a manner peculiar to this species and to A. cicutaria of subg. Anemiorrhiza.

20. Anemia wightiana Gardner, Calc. Jour. 7:10 t.1. 1847 (Pl. XXI, Fig. B).
Hemianemia schimperiana var. wightiana (Gardner) Reed, Bol. Soc. Brot. II. 21:162. 1948.

Rhizome apex ascending and clothed with petiole bases, 1.0-1.5 cm thick; hairs orange; fronds caespitose; stipe terete, 4-22 cm long, 1-3 mm broad, orange to light brown, villous; blade oblong-deltoid-ovate, bipinnate to bipinnate-pinnatifid, chartaceous, 7-15 cm long; pinnae 8-13 pairs; pinnules ovate-obtuse, lobes entire and rounded, hirsute to tomentose; fertile pinnae petiolate, erect, approximate or subapproximate to the sterile pinnae, shorter than the sterile blade; spores 91-107 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, spongy-medullate.

Distribution. Southern India (Pl. VII, Fig. A).

Type collection. "In an open bushy, rocky place, below Sispara, on the Malabar slopes of the Neelgherries, at an elevation of about 5000 feet, February 1845, Gardner and Wight."

Specimens examined. INDIA. NILGIRIS DISTRICT: Sispara Ghat, Gamble 13407 (K); Koondah Ghat, Gough 3232(57) (K); Nilgiri Mountain,

somewhat exceeding the sterile blade, dense or "bushy"; spores 75-110 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. Minas Gerais, Brazil (Pl. VIII, Fig. B).

Type collection. Sturm cites two specimens with his description of A. imbricata: "In Brazilia orientali: Sellow in Herb. Berol.(B. n. 671. c. 18 et 3b. 11); in Minas Geraes; Gardner 5341." I have seen no specimens of the Sellow collection, and since the three specimens of Gardner 5341 examined closely match Sturm's description, I am designating the specimen of the latter at K (!) as the lectotype. The original may be in the Martius Herbarium at BR, the Gardner Herbarium at K, of the Sturm Herbarium (loc. ?).

Specimens examined. BRAZIL. MINAS GERAIS: Bello Horizonte, Brade 11823 (R); Diamentina, Brade 13943 (RB), Brade 13944 (RB); Jaboticatubas, 10 km. n. of Lagôa Santa, km. 56 on the road from Bello Horizonte to Conçeicão, L.B. Smith 6945 (MO); Martinsio, Perrotet 1854 (BR); Ouro Preto, Damazio, no date (RB no. 36937)(RB); campos pres Saramenha, Damazio 1424 (P), Damazio 1426 (MICH), Damazio 1438 (P), Damazio 1438 (P); Serra do Cipó, Palácio, Duarte 2041 (RB); Serra do Cipó, Heringer e Castellanos 22.021 (R); Serra do Curral, Prope Bello Horizonte, Silveira 114 (R p.p.); Serra de Cural del Rey, Gardner 5341 (K, lectotype); Serra do Frio, Gardner 5341 (BM, isolectotype); Serra da Piedade, Claussen [Galeotti] 67 (RB); Damazio 1939 (MICH); Gardner 5341 (FI, isolectotype); Gardner no date (BM).

Discussion. Anemia imbricata is very similar to A. villosa and is probably a derivative from it. Its broader outline, coriaceous texture, and bushy fertile pinnae are distinctive features, but there is great variation which has led to confusion between the two. The broadest forms have been confused with A. raddiana and the broad form of A. villosa.

27. Anemia blechnoides Brade, Arq. Jard. Bot. [Rio de Janeiro] 11:33 t. 12. 1951 (Pl. XXIV, Fig. B).

Rhizome horizontal, 1.5 cm thick; hairs maroon; fronds caespitose; stipe terete, flattened at the base, 4-19 cm long; 2 mm broad, yellow, hirsute with stiff black hairs; blade linear-lanceolate, once pinnate, coriaceous, 10-22 cm long; pinnae 14-26 pairs, entire, lanceolate, subglabrous; fertile pinnae petiolate, erect, approximate to the sterile pinnae, ca. equal in length to the sterile blade; spores 78-91 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. Espírito Santo, Brazil (Pl. VIII, Fig. B).

Type collection. "Brasilia, Estado do Espírito Santo, Forno Grande, Municipio Castelo, 1,200 m.s.n. do mar. A. C. Brade 19833, 15 May 1949." Brade reports the type to be at RB.

Specimens examined. BRAZIL. ESPIRITO SANTO: Castelo, Forno Grande, Brade 19833 (RB, isotype).

Discussion. In its once pinnate construction, Anemia blechnoides resembles A. organensis, but it is distinct in several respects: the maroon rhizome hairs, the short stipe, stiff black stipe hairs, coriaceous texture, and origin of fertile pinnae approximate to the sterile pinnae. It probably had an origin independent from that of A. organensis.

28. Anemia retroflexa Brade, Anais Prim. Reun. Sul-Am. Bot. Rio de Janeiro 2:9. t. 5. 1938 (Pl. XXV, Fig. A).
Hemianemia retroflexa (Brade) Reed, Bol. Soc. Brot. II. 21:162. 1948.

Rhizome horizontal, 2.0-2.5 cm thick; hairs maroon; fronds caespitose; stipe flattened, 14-28 cm long, 2-3 mm broad, yellow, pilose; blade deltoid, bipinnate-pinnatifid, chartaceous, 11-15 cm long; pinnae 12-15 pairs, strongly retroflexed from the rachis; segments ovate-obtuse, hirsute; fertile pinnae petiolate, erect, subapproximate to the sterile pinnae, ca. the same length as the sterile blade; spores 91-98 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth, solid.

Distribution. Rio de Janeiro, Brazil (Pl. VIII, Fig. B).

Type collection. "Brasilia, Edo. do Rio de Janeiro, Serra da Fumaça, Mun. de Sta. Magdalena, 19 September 1935, J. de Santos Lima 328." Brade reports the type to be at RB.

Specimens examined. BRAZIL. ESPIRITO SANTO: Pedra de Corrego Sautini, perto de Baunilha, Huffman, no date (RB no. 78348) (RB). RIO DE JANEIRO: Sta. Magdalena, Serra da Fumaça, Santos Lima 328 (US, isotype).

Discussion. The most distinctive feature of this species is the retroflexed pinnae. It is the only occurrence of this character in the genus although it is found in several other genera of ferns. The flattened stipe is also distinctive, but it lacks the lateral grooves found in the other species with flattened stipes, such as A. gardneri. Actually it is slightly convex on the abaxial surface and appears much like the flattened petiole bases of certain specimens of A. organensis and A. villosa. It is probably related to the A. villosa group of species on the basis of its stipe, thick rhizome, solid spore ridges, and other details of spore and leaf morphology.

29. Anemia simplicior (Christ) Mickel comb. nov. (Pl. XXV, Fig. B).
Anemia anthriscifolia var. simplicior Christ, Fedde Rep. Sp. Nov. 6:351. 1909.
Hemianemia anthriscifolia var. simplicior (Christ) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Rhizome horizontal, 0.5-1.5 cm thick; hairs maroon; fronds caespitose; stipe terete, 7-55 cm long, 1-2 mm broad, yellow to light brown, occasionally partly dark purple, pilose to subglabrous; blade deltoid-ovate, bipinnate to bipinnate-pinnatifid, chartaceous, 9-25 cm long; pinnae 10-16 pairs; pinnules remote, ovate to lanceolate, broadly adnate, lobed to pinnatifid, pilose; large unicellular trichomes centrally attached; fertile pinnae petiolate, erect, remote from the sterile pinnae, slightly exceeding the sterile blade; spores 65-81 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges subverruculate, spongy-medullate.

Distribution. Northeastern Argentina, Paraguay, and southeastern Brazil (Pl. IX, Fig. D).

Type collection. "Paraguay, Sierra de Anambay, ad margines silvarum

pr. Punta Porá, Hassler 10452, leg. Rojas." The type was not seen and is probably either in the Christ herbarium at P or in the Hassler collection at G.

Selected specimens examined. ARGENTINA. CHACO: Mocoví, Santafecino, Venturi 22 (FI). CORRIENTES: Mburucuya, Estancia Santa Teresa, Pedersen 375 (BR, K, MO, US). FORMOSA: Jorgensen 3272 (US). MISIONES: Loreto, Burkart 1463 (GH); Candelaria, Loreto, Montes 1806 (GH, K); Salto del Yguazú, Osten and Rojas 7260 (S-PA); San Ignacio, Ceyucuvre, Montes 2082 (GH, MO).

BRAZIL. PARANA: Iguazú, Beetle 2191 (MO, US). RIO GRANDE DO SUL: Ferromecco, Vumers 9 (US); Rio Pardo, Fazenda Leitão, Jurgens 28 (NY, UC); Santa Cruz, Jurgens (Rosenstock no. 221) (DEN, MICH, S-PA, US); Santa Maria, Palacios-Cuezzo 1656 (RB); São Leopoldo, Eugenio 1460 (GH, RB); Tranbudo, St. Angel, Watschaske 52 (S-PA). SANTA CATARINA: Lages, Spannagel (Rosenstock no. 221a) (NY, RB, US); Pora Teutonia, Ploumann 440 (RB).

PARAGUAY. In valle fluminis Y-acá, prope Palenzuela, Hassler 6900 (G, NY); Montes Encarnación, Hassler 1414 (G); Paraná, in regione fluminis Alto Paraná, Fiebrig 6476 (GH, US); in regione Yerbalium de Maracajú, Paraguaria euro-austra, Hassler 5883 (BM); Pacoba, Hassler 5883 (G, NY); in viciniis Caaguazú, Hassler 9070 (BM, G, GH, NY); Sierra de Amambay, Ponta Porá, Rojas (Hassler no. 10452) (G, isotype); Villarrica, Jorgensen 4065 (G, GH, MO, NY, US); Río Pilcomayo, Kerr, in 1890-91 (K).

Discussion. The most distinctive feature of Anemia simplicior is the media attachment of its large unicellular trichomes (Pl. II, Fig. C_4). These are found nowhere else in the genus. Previously this species has been treated as a variety of A. anthriscifolia [= A. tomentosa], which it resembles in its dissection. However, there are several characters which mark it as a distinct species: its maroon rhizome hairs; medially attached trichomes; distinct, remote pinnules; and more contorted epidermal cells. Furthermore, young sporophytes of A. simplicior are more dissected than those of A. tomentosa.

Anemia simplicior forms a distinct group with A. raddiana and A. bartlettii. They are all relatively large plants, with maroon rhizome hairs, bipinnate to bipinnate-pinnatifid fronds, contorted epidermal cells, and long, slender fertile pinnae that are remote from the sterile pinnae.

30. Anemia raddiana Link, Hort. Berol. 2:144. 1833 (Pl. XXVI, Fig. A).
Aneimia flexuosa α Prantl, Schiz. 94. 1881.

Rhizome horizontal, 1-2 cm thick; hairs maroon; fronds caespitose; stipe terete, 14-42 cm long, 1-3 mm broad, yellow, pilose to hirsute; blade deltoid-ovate, bipinnate, chartaceous to subcoriaceous, 10-25 cm long; pinnae 10-15 pairs; pinnules broadly adnate, usually approximate, oblong, rhomboidal to rounded, entire to crenate, pilose; large unicellular trichomes with attachment submedial to subbasal; fertile pinnae petiolate, erect, remote or subremote from the sterile pinnae, slender, exceeding the sterile blade; spores 81-97 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges smooth to slightly verruculate, with slightly spongy medulla.

Distribution. Southeastern Brazil (Pl. IX, Fig. D).

Type collection. Link cites no specimens but refers to an illustration of "A. flexuosa" by Raddi (Pl. Bras. 1:71. t. 13. 1825). This drawing is not a perfect match for the average specimens of this species, but does seem to resemble this more than the broad form of A. villosa. The great variation both in A. raddiana and A. villosa make it difficult to determine the identity of the type for certain, but the evidence from the illustration and the original description more strongly suggest the correctness of my interpretation.

Selected specimens examined. BRAZIL. MINAS GERAIS: Bello Horizonte, Serra do Rola Moco, Foster and Foster 552 (US); Carandai, Quebiacambão, Duarte 895 (MICH); Diamantina, Pereira 1368 (MICH); Joboticatubas, 10 km. n. of Lagâo Santa, L.B. Smith 6945 (R, US); São Sebastião do Paraíso, Baixada do Mourá, Vidal I-686 (R); Viçosa, Mexia 4390 (BM, F, G, GH, K, MICH, MO, NY, UC, US). PARANA: Capão Grande, Dusen 3975 (BM, R); Itaperassú, Dusen 13864 (US); Jaguariahyva, Dusen 11617 (S-PA); Morungava, Dusen 16480 (GH); Piraquara, Estrada a Monte Alegre, Hatschbach 1911 (RB); Restinga Secca, Dusen 3098 (NY, R). RIO DE JANEIRO: Corcovado, Rose 21274 (NY, US); Nova-Friburgo, Leite 4236 (MO); Organ Mountains, Gardner 7 (BM, G); Sta. Thereza, Dusen 1927 (G, GH, R, US); Serra de Itatiaya, Brade 10326 (R); Serra Estrella, Costa Gama, Luetzelburg 307 (MICH, UC). RIO GRANDE DO SUL: Bocca do Monte, Palacios-Cuezzo 2439 (RB); Rio Pardo, Fazenda Ayre, Jurgens 283 (NY, UC); Santa Cruz, Jurgens 283 (S-PA); São Leopoldo, Emita São Manoel, Dutra 166 (R). SANTA CATARINA: Biguassú, Antonio Carlos, Reitz 270 (GH, HBR, RB, US); Florianópolis, Paulo Lopes, Spannagel 329a (HBR, S-PA); Itacorobi, Ilha de Santa Catarina, Rohr 297 (HBR, RB); Joinville, Schmalz 103 (F, MO, NY, S-PA); Lages, Morro Grande, Spannagel 13 (HBR, S-PA, US). SAO PAULO: Campo Grande, L.B. Smith 1988 (GH); Capivary, Gerdes 115 (NY, UC); Jaraguá, Brade 5817 (S-PA); Tamandaré 350 (RB); Rio Grande, Wacket 37 (NY, S-PA); São Paulo, Villa Emma, Brade 16050 (G, MICH, NY).

Discussion. Anemia raddiana resembles A. simplicior in its maroon rhizome hairs, contorted epidermal cells, and origin of the fertile pinnae remote from the sterile pinnae. It also frequently has unicellular trichomes with a submedial attachment, perhaps representing an intermediate stage in the evolution of the medial attachment as found in A. simplicior. Its larger spores and stomates strongly indicate a polyploid condition in A. raddiana, while A. simplicior is apparently diploid.

31. Anemia bartlettii Mickel, sp. nov. (Pl. XXVI, Fig. B).

Rhizomate horizontale, 1.0-1.5 cm crasso; pilis atrorufis; foliis caespitosis; petiolo tereti, 8-45 cm longo, 1-2 mm lato, stramineo vel interdum partim atropurpureo; lamina deltoido-ovata, bipinnata vel bipinnata-pinnatifida, 14-28 cm longa, chartacea; pinnis 11-16 = jugis; pinnulis late adnatis, oblongo-obtusis, lobatis vel pinnatifidis, pilosis; pinnis fertilibus petiolatis, erectis, remotis a pinnis sterilibus, eadem fere longitudine qua lamina sterilis; sporis 85-98 μ, tetrahedro-globosis, angulorum umbonis conspicuis, liris levibus, spongio-medullatis.

I dedicate this species to the late Harley Harris Bartlett (1886-1960), botanical explorer and Professor of Botany at the University of Michigan.

Distribution. British Honduras (Pl. IX, Fig. A).

Type collection. British Honduras, El Cayo District, ravine, Mountain Pine Ridge, 3 March 1931, H.H. Bartlett 11898.

Specimens examined. BRITISH HONDURAS. El Cayo District, Mountain Pine Ridge, Bartlett 11898 (MICH, type; MICH, UC, US), Hunt 428 (US).

Discussion. Anemia bartlettii seems to be most closely related to A. simplicior, which it resembles in its maroon rhizome hairs, chartaceous texture, origin of the fertile pinnae remote from the sterile pinnae, contorted epidermal cells, and conspicuously spongy-medullate spore ridges.

The geographical disjunction between this species and A. simplicior is the same as that found in A. (subg. Anemia) hirta. This new species also adds to the number of endemic species of Anemia occurring in Mexico and Central America, and further exploration in these areas may reveal even more.

32. Anemia flexuosa (Savigny) Swartz, Syn. Fil. 156. 1806 (Pl. XXVII, Fig. A).
Osmunda flexuosa Savigny in Lam. Enc. 4:652. 1797.
Aneimia flexuosa δ setosa Prantl, Schiz. 95. 1881.
Hemianemia flexuosa (Savigny) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Rhizome apex ascending and covered with petiole bases, 0.5-1.5 cm thick; hairs orange to reddish-orange; fronds caespitose; stipe terete, sometimes flattened at the base, 8-42 cm tall, 1-2 mm broad, yellow, hirsute with stiff black hairs or densely clothed with long orange hairs; blade deltoid-ovate, bipinnate to bipinnate-pinnatifid, chartaceous to subcoriaceous, 10-26 cm long; pinnae 6-13 pairs; pinnules broadly adnate, ovate to oblong, obtuse, subglabrous to hirsute; fertile pinnae petiolate, erect, remote from the sterile pinnae, usually shorter than the sterile blade; spores 87-107 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges slightly to markedly verruculate, spongy-medullate.

Distribution. Western South America from Bolivia to Colombia (Pl. IX, Fig. D).

Type collection. Savigny bases this species on a specimen seen in the Jussieu herbarium, but gives no collection data with which the type can be distinguished. At the end of the description he says, "Cette plante croit ...", indicating that he probably did not know where the plant came from. I have seen a photograph of a specimen (of what I construe as A. raddiana) from Rio de Janeiro in the Jussieu herbarium (from Herb. Dombey), but it is doubtful that this is the type since Savigny made no mention of further data. His description seems to apply best to the species found in western South America, but it could also apply conceivably to A. raddiana or the broad form of A. villosa. Since Bernard de Jussieu spent a number of years collecting plants in Bolivia and Peru, and many of his specimens found their way ultimately to the herbarium of A.L. de Jussieu, it is quite possible that the type is one of his collections. Furthermore, Swartz (1806) cited A. flexuosa as coming from Peru. The real type specimen may be misplaced.

Selected specimens examined. BOLIVIA. COCHABAMBA: Chapare, Incachaca, Steinbach 9133 (GH, K, NY, S-PA, UC); Tunari, Kuntze 4/51892 (NY). LA PAZ: Apolo, Williams 1364 (GH NY, UC, US); Hacienda Simaco sobre el camino a Tipuani, Buchtien 5117 (F, S-PA, US); Sorata, Rusby 118 (NY); Nord-Yungas, Milluguaya, Buchtien 793 (BM, F, G, MO, NY, US); Yungas, Bang 304 (BM, G, GH, K, MO, NY, US). SANTA CRUZ: Lagunillas, Cordillera of Tucahuasi, Cardenas 2838 (F); Cordillera de Sta. Cruz, in der Buschregion von Tres Cruces, Herzog 1554 (G, UC, US).

COLOMBIA. CALDAS: near La Dorada, Haught 2104 (US). MAGDALENA: Caracoli, André 512 (K). TOLIMA: Marquita, Haught 2423 (GH, UC, US); Honda, Pennell 3569 (F, MO, NY, US).

ECUADOR. BOLIVAR: Road above Balzapamba, Haught 3304 (GH). CHIMBORAZO: Cañon of the Río Chanchan, about 5 km. n. of Huigra, Camp E-3370 (F, GH, MO, NY, RB, UC, US).

PERU. AYACUCHO: Ccarrapa, between Huanta and Río Apurimac, Killip & A. C. Smith 22319 (NY, US). CUZCO: Calca, Valle Lares, Bües 1887 (US); Lucumaya Valley, Cook & Gilbert 1383 (US); Machupicchu, Coronado 133 (MICH, UC); Quillabamba, Coronado 117 (UC, US); San Miguel, Urubamba, Cook & Gilbert 614a (US). HUANUCO: Valley of Huanuco, Muña, Pearce 125 (BM, K). JUNIN: Huacapistana, Killip & A. C. Smith 24152 (F, NY, US); in Mont. Pariahuanca, Mathews 1111 (BM, K, NY). SAN MARTIN: Chachapoyas, Sesuya, [probably Mathews] 3300 (K). VILCABAMBA: Hacienda on Río Chinchao, Macbride 4985 (F, US).

Discussion. The most striking features of Anemia flexuosa are the elongate deltoid shape of the blade, the oblique rhizome, and frequently the stiff, black hairs on the stipe. It was on these hairs that Prantl based his name A. flexuosa var. setosa.

Anemia flexuosa resembles A. tomentosa var. australis in being bipinnate with large segments, orange rhizome hairs, origin of the fertile pinnae remote from the sterile pinnae, the fertile pinnae shorter than the sterile blade, and in the verruculate spores. Spore and stomate sizes suggest that it is a polyploid species.

Anemia flexuosa is composed of three elements which are geographically distinct. The most abundant collections are from Peru and Bolivia. The few collections from Ecuador are more divided (bipinnate-pinnatifid), the segments are rounded, the spores are extremely verruculate, and the larger spores and stomates indicate a higher genomic level.

In Colombia the plants have long, lax, orange hairs on the stipe, and the fertile pinnae arise in a position varying from remote to approximate to the sterile pinnae, the fertile pinnae often exceeding the sterile blade. The spore ridges are only slightly verruculate. As in A. villosa, this is probably best treated as a single species, but further collections are needed in the northern part of the range to evaluate better these variations.

33. Anemia tomentosa (Savigny) Swartz.

Rhizome horizontal; hairs orange; fronds caespitose to scattered; stipe 1-2 mm broad, yellow to dark purple, subglabrous to tomentose; blade deltoid-ovate to ovate, bipinnate to bipinnate-pinnatifid, chartaceous to subcoriaceous; fertile pinnae remote to approximate to the sterile

pinnae, shorter than or exceeding the sterile blade; spore ridges smooth to subverruculate, spongy-medullate; reproduction sexual or apogamous.

Anemia tomentosa is an extremely widespread and variable species, and is held together largely on the basis of its orange rhizome hairs and chartaceous to subcoriaceous texture of the lamina. The species can be divided into four varieties, which show varying degrees of similarity to A. ferruginea, a species often confused with A. tomentosa.

33a. Anemia tomentosa (Savigny) Swartz var. tomentosa (Pl. XXVII, Fig. B).

Osmunda tomentosa Savigny in Lam. Enc. 4:652. 1897.
Osmunda fulva Cav., Icon. 6:70 t. 593 f. 2. 1801.
Osmunda deltoidea Cav., Icon. 6:70 t. 593 f. 1. 1801.
Anemia deltoidea (Cav.) Swartz, Syn. Fil. 156. 1806.
Anemia tomentosa (Savigny) Swartz, Syn. Fil. 157. 1806.
Anemia fulva (Cav.) Swartz, Syn. Fil. 157. 1806.
Aneimia cheilanthoides Kaulf., Enum. 53. 1824.
Aneimia villosa α deltoidea (Cav.) Presl, Suppl. Tent. Pterid. 82. 1845.
Aneimia villosa δ tomentosa (Swartz) Presl, Suppl. Tent. Pterid. 83. 1845.
Aneimia villosa ε cheilanthoides (Kaulf.) Presl, Suppl. Tent. Pterid. 83. 1845.
Anemia tomentosa ε cheilanthoides (Kaulf.) Moore, Ind. Fil. 70. 1857.
Anemia anthriscifolia var. rotundata Lindman, Arkiv. Bot. 1:258 t. 12 f. 1. 1903.
Hemianemia tomentosa (Savigny) Reed, Bol. Soc. Brot. II. 21:161. 1948.
Hemianemia anthriscifolia var. rotundata (Lindman) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Rhizome horizontal, short-creeping, internodes up to 2 cm long, up to 0.8 cm thick; hairs orange; fronds scattered; stipe terete, 3-40 cm tall, ca. 2 mm broad, usually yellow, rarely darkly pigmented, subglabrous to tomentose; blade ovate or deltoid-ovate, bipinnate-pinnatifid, chartaceous to subcoriaceous, 5-20 cm long; pinnae 11-17 pairs; pinnules broadly adnate, oblong, deeply pinnatifid, lobes rounded, tomentose; marginal spicules occasionally present; the subbasally attached unicellular hairs short, ovate; fertile pinnae petiolate, erect, approximate to the sterile pinnae, usually equal to or slightly exceeding the sterile blade; spores 91-159 μ, tetrahedral-globose, frequently abortive and irregular, the angle protuberances conspicuous or inconspicuous, the ridges subverruculate, spongy-medullate; reproduction probably apogamous.

Distribution. Uruguay, Paraguay, northeastern Argentina, and southeastern Brazil (Pl. IX, Fig. C).

Type collection. Argentina, "Buenos-Ayres, Commerson," I have seen photographs of the type, which is in the Lamarck Herbarium at P. I have not seen the type.

Selected specimens examined. ARGENTINA. BUENOS AIRES: Sierra del Chaco, Lorentz, Feb.-April 1881 (FI, G, US); Sierra de la Ventana,

Partido de Tornquist, Cabrera 5215 (GH). MISIONES: Candelaria, Bella Vista, Bertoni 2329 (MO); Posadas, Bonpland, Ekman 60 (MO, NY, S-PA).

BRAZIL. PARANA: Villa Velha, Rizzini e Lab 630 (RB). RIO DE JANEIRO: Riedel (R no. 1431) (NY). RIO GRANDE DO SUL: Neu-Württemberg, Arroio Alegre, Bornmüller 315 (GH, S-PA); Santa Cruz, Picc. Nore Tomern, Jurgens 57 (Rosenstock 271) (NY, P, RB, UC, US). SANTA CATARINA: Orleães, Sta. Clara, Reitz C1741 (HBR, RB, US); Lages, Capão Alto, Spannagel 26 (Rosenstock II 235) (DEN, HBR, NY, S-PA, UC, US).

PARAGUAY. Cordillera de Altos, Hassler 490 (G).

URUGUAY. FLORES: Río Ti y A. Carjiuteria, Rosengurtt B1530 (GH, NY, US). LAVALLEJA: Aigua, Herter 94494 (GH, MO, RB); Cerro Grande, between Salus and Minas, Bartlett 20888 (GH, UC). MALDONADO: Cerro Animas, Herter 99574 (US); Cerro Pan de Azúcar, Berro 5171 (BM). MINAS: Cerro Areguita, Osten 4479 (S-PA). MONTEVIDEO: Cerro de Montevideo, Gibent 605 (US); Colon-LaPaz, Herter 78503 (S-PA, US). RIVERA: Cuñopiru, Estancio Sloan, Wright, in 1933 (BM). SALTO: Osten 5453 (S-PA, US). SORIANO: Juan Jackson, F.C.C.V., Rosengurtt B 1482 (GH, US). TACUAREMBO: Valle Eden, Herter 3710 (GH). TREINTA Y TRES: Yerbal, Herter 83361 (S-PA).

Discussion. Through most of its range this variety can be distinguished by its ovate blade outline, greater number of pinnae, rounded pinnule lobes, stout, yellow stipe and fertile pinnae about equalling the sterile blade in height. There is frequent spore abortion in most specimens, and judging from its resemblance in spore irregularities to those in var. anthriscifolia, it is apogamous in reproduction. There are a few specimens with small uniform spores and stomates, in contrast to the usual large ones of the variety, and these specimens may represent a sexual element within the group.

This variety is also similar to var. anthriscifolia in characters other than the spores, such as the short, ovate trichomes, occasional marginal spicules, and the fertile pinnae approximate to the sterile pinnae. The two varieties are difficult to distinguish in Paraguay and in some specimens from Brazil. It is not to be expected that two apogamous species can hybridize, but if one or both have sexual elements (see above), then crossing is possible. I do not know whether these apparently intermediate specimens are the result of hybridization, or whether they represent the ancestral stock from which more typical members of the two varieties have arisen by somatic mutation, or whether this is part of their natural variation pattern.

33b. Anemia tomentosa (Savigny) Swartz var. anthriscifolia (Schrader) Mickel, comb. nov. (Pl. XXVII).

Anemia anthriscifolia Schrader, Gött. gel. Anz. 1824:625. 1824.

Anemia flexuosa var.? anthriscifolia (Schrader) Kze., Linnaea 18:308. 1844, attributed erroneously to Schrader. As to basionym, not as to specimen cited (Leibold, Mexico).

Anemia ferruginea H.B.K. var. anthriscifolia (Schrader) Kze., Linnaea 23:222. 1850, as to basionym at least, excl. syn. A. fulva var. mexicana and loc. Mexico.

Hemianemia anthriscifolia (Schrader) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Rhizome horizontal, compact to short-creeping, up to 0.7 cm thick; hairs orange; fronds scattered, stipe terete, 3-33 cm long, ca. 1 mm broad, at least partly dark brown or purple, rarely entirely yellow, pilose to hirsute; blade deltoid to deltoid-ovate, bipinnate to bipinnate-pinnatifid, chartaceous to subcoriaceous, 6-18 cm long; pinnae 8-13 pairs; pinnules broadly adnate, ovate, often pinnatifid; lobes obtuse to acute, pilose to hirsute; marginal spicules occasional; the subbasally attached unicellular hairs ovate; fertile pinnae petiolate, erect, approximate to the sterile pinnae, usually greatly exceeding the sterile blade; spores 85-172 μ, tetrahedral-globose, the angle protuberances inconspicuous, frequently abortive and irregular, the ridges smooth to subverruculate, spongy-medullate; reproduction apogamous; chromosomes somatic and meiotic = 114.

Distribution. Northern Argentina, Bolivia, Paraguay and southeastern Brazil (Pl. IX, Fig. C).

Type collection. Brazil, Bahia, "prope Barra da Vareda, Pr. Max. Neovid., in 1820." (BR!).

Selected specimens examined. ARGENTINA. CHACO: Col. Benítez, Schultz 739 (GH). CORDOBA: near Cassaffousth, Rose 21049 (NY, US). CORRIENTES: Cachoeira do Campo, Stephan 69 (F, G). FORMOSA: Pirané, Casco Tue, Morel 821 (BM). MISIONES: Candelaria, Santa Ana, Montes 1384 (US). SALTA: Caldera, Mojotoro, Meyer 3686 (GH). SANTIAGO DEL ESTERO: El Chearco, Venturi 10372 (MO, NY, S-PA).

BOLIVIA. AYOPAYA: Sailapata, Cárdenas 3063 (US). COCHABAMBA: Mizque, on mule trail between Chaguarani and Quioma silver mines, Eyerdam 25094 (F, UC). LA PAZ: Larecaja, viciniis Sorata, cerro del Iminapi, Mandon 1599 (G, GH, K, S-PA). SANTA CRUZ: Chaco, between Charagua and Izozog, Cárdenas 2580 (US). TARIJA: Narvaez, Cárdenas 4936 (US).

BRAZIL. BAHIA: prope Barra da Vareda, Pr. Max. Neovid., in 1820 (BR, type); Agreja velha, Blanchet 3270 (BM, G, K, MO, NY p.p., RB). ESPIRITO SANTO: Vitoria, Brade 18091 (NY, R, RB). MATTO GROSSO: Corumbá on Rio Paraguay, Chase 11120 (US); Cuyaba, Hoehne 4948 (UC). PARAIBA: Alagôa Grande, de Moraes 835 (US). PERNAMBUCO: Herva dos lagidos, Pickel 1028 (R); Tapera, Pickel 2964 (F, GH, MICH, US). RIO DE JANEIRO: Nitheroy, Dusen 146 (G, GH, MO, US); Organ Mts., Gardner 89 (BM, FI, G); vicinity of Rio de Janeiro, near Corcovado, Rose 20164 (GH, NY, US). RIO GRANDE DO SUL: Porto Alegre, Reineck and Czermak 168 (S-PA); Estevão Resenda, Stier 57 (S-PA). SAO PAULO: Concesão dos Guaralhos, Brade 6929 (S-PA); Insul. S. Sebastiani, Casaretto 120 (P).

PARAGUAY. Cerro Pelado, pres de Paraguari, Balansa 2925 (BM, F, K, S-PA, US); Cordillera de Altos, Hassler 3000 (BM, G, GH, K, NY, P); Chaco Paraguayo, Fuerte Olimpo, Rojas 13641 (BM, MO); L'Assomption, Balansa 332 (BR, P, S-PA); in viciniis Caaguazú, Hassler 9215 (BM, G, GH, NY, UC).

Discussion. This is the most widespread variety of A. tomentosa, and can usually be distinguished from the other varieties by the combination of its deltoid blade, acute pinnule lobes, slender, often darkly pigmented stipe, and fertile pinnae far exceeding the sterile blade in height. In Brazil it is confused with A. ferruginea var. ahenobarba, but the latter can be identified by its red to maroon rhizome hairs and coriaceous texture.

Anemia tomentosa var. anthriscifolia is a hexaploid, indicating an origin involving a tetraploid and diploid. The resulting triploid in all probability would have been sterile, and a hexaploid could have been produced by allopolyploidy. Hexaploidy is not necessarily correlated with apogamy in this group, for var. mexicana, also a hexaploid, is sexual.

The specimens of Anemia tomentosa from Bolivia do not match perfectly any of the four varieties, but I have placed them in var. anthriscifolia on the basis of their acute pinnule lobes, fertile pinna position usually approximate to the sterile pinnae, and the ovate shape of the subbasally attached unicellular hairs. The spores and stomates of some of them are small and in the range of diploid measurements. As in var. tomentosa, these may represent elements which have contributed to the evolution of the four recognized varieties.

33c. Anemia tomentosa (Savigny) Swartz var. australis Mickel, var. nov. (Pl. XXIX, Fig. A).

Rhizomate horizontali, compacto, usque ad 0.8 cm crasso; pilis aurantiacis; foliis nunc dispersis nunc caespitosis; petiolo tereti, 4-32 cm longo, 1.0-1.5 mm lato, piloso vel hirsuto; lamina deltoido-ovata, bipinnata vel paene bipinnata-pinnatifida, chartacea, 5-17 cm longa; pinnis 5-13=jugis; pinnulis late adnatis ovato-obtusis, non profunde incisis; lobis acutis, pilosis; trichomatibus cum adnationibus subbasalibus lineari-oblongis; spiculis marginalibus nullis; pinnis fertilibus petiolatis, erectis, remotis a pinnis sterilibus, eadem fere longitudine qua lamina sterilis; sporis 68-91 μ, tetrahedro-globosis, uniformibus et regulàribus, angulorum umbonis conspicuis, liris levibus vel subverruculatis, spongiomedullatis; propagatione sexuali; chromosomatum numero 2n = 76.

Distribution. Northwestern Argentina (Pl. IX, Fig. C).

Type collection. Argentina, Córdoba, Tauti, II-1944, Delio Abbiotti 1043 (US!).

Selected specimens examined. ARGENTINA. CATAMARCA: Los Bajanes, Peirano, 24 April 1935 (GH); Andalgala, Esquina Grande, Schreiter 1182 (F). CORDOBA: Colón, Agua de Oro, Dawson 619 (GH, NY); Santa Maria, Estancia Los Molles, Pierotti 5086 (GH, MO); Tauti Abbiotti 1043 (US, type; GH). JUJUY: Jujuy, Parodi 9778 (GH); Río Yala 15 km. w. of Yala, West 6252 (GH, MICH, MO, UC). LA RIOJA: cerca de Las Canas, camino al Cantadero, Hunziker 5065 (GH); La Rioja, Giacomelli (LIL no. 20494) (F, GH). SALTA: R. de Lerma, Campo Quijano, Meyer 3688 (GH); Los Potreros am Fuss des Nevado del Castillo, Lorentz and Hieronymus 163 (BM, NY). SAN LUIS: Junin, Piedra Blanca: Ladera occidental del Comechingones, coll. unknown, 2161 (GH); Los Molles, near Merlo, Wright, in 1933 (BM). TUCUMAN: Río Chico, El Potrerillo, Monetti 1533 (F, GH); Tafi, Yerba Buena, Venturi 205 (GH, US).

Discussion. Although var. australis has never before been given a name, it is probably the most distinct variety of the species. The pinnules are less divided and more obtuse than in the other varieties, and the position of the fertile pinnae remote from the sterile pinnae separates it from vars. tomentosa and anthriscifolia. It is always chartaceous in texture; the subbasally attached unicellular trichomes are linear-oblong; and the marginal spicules are lacking. The variety is diploid and sexual.

33d. Anemia tomentosa (Savigny) Swartz var. mexicana (Presl) Mickel, comb. nov. (Pl. XXIX, Fig. B).

Aneimia flexuosa var.? anthriscifolia sensu Kunze, Linnaea 18:308. 1844, as to specimen cited, not basionym.

Aneimia fulva γ mexicana Presl, Suppl. Tent. Pterid. 84. 1845.

Rhizome horizontal, compact to short-creeping; hairs orange; fronds scattered; stipe terete, 5-24 cm long, ca. 1 mm broad, yellow to light brown, subglabrous to hirsute; blade deltoid-ovate, bipinnate-pinnatifid, chartaceous to subcoriaceous, 4-15 cm long; pinnae 6-13 pairs; pinnules narrowly adnate, ovate; lobes acute, pilose to hirsute; the subbasally attached trichomes linear; marginal spicules lacking; fertile pinnae, petiolate, erect, remote or approximate to the sterile pinnae, about equal to the sterile blade in height; spores 78-110 μ, tetrahedral-globose, uniform and regular, the angle protuberances conspicuous, the ridges subverruculate, spongy-medullate; reproduction sexual; chromosomes n = 114.

Distribution. Mexico, from Sonora and Tamaulipas to Oaxaca (Pl. IX, Fig. C).

Type collection. "In regione subtropica Mexici orientalis, Leibold pl. mex. exs. sine num." The type which wss referred by Kunze to A. flexuosa var.? anthriscifolia, was probably in the Kunze collection at Leipzig, which was destroyed in the Second World War.

Selected specimens examined. COLOMBIA. MAGDALENA: w. of Valledupar, Haught 3903a (US).

HAITI. Vicinity of Jean Rabel, uplands above Mole Road, Leonard & Leonard 13035 (K, RB, US).

MEXICO. CHIHUAHUA: Vicinity of Areponapuchic, slopes of Barranca de Urique, Knobloch 1377 (US); Batopilas, Palmer 91 (BM, GH, MO, NY, US). DURANGO: La Bajada Tamazula, Ortega 4294 (US). JALISCO: moist slopes near Guadalajara, Pringle 1834 (BM, BR, F, G, GH, MICH, NY, S-PA, UC, US); barrancas, w. of La Quemada, Pennell 19897 (US). NAYARIT: La Barranca, Jones 23473 (GH, MO, UC). OAXACA: Fortín, Conzatti 1614 (F); Distrito del Centro, Pozas Zarcas, Conzatti 4155 (US). PUEBLA: Tlacuiloltepec, Purpus 4045 (UC). SAN LUIS POTOSI: Valle de Mexico, Schaffner 26 (BM, NY); in montibus Escalerillas, Schaffner 945 (GH). SINALOA: Cerro Colorado, Brandegee, 1 Nov. 1904 (GH, UC); Piedras Azules, Choix, Ortega 3093 (US). SONORA: Sierra del Nacori, Hartman 345 (GH, NY); La Mina Verde, 31 km. de Cumpas, Wiggins 7398 (MICH, UC, US). TAMAULIPAS: Cerro de los Armadillos, vicinity of San José, Bartlett 10390 (MICH); vicinity of Marmolejo, above El Rosario, Bartlett 10866 (MICH, US). VERA CRUZ: Zacuapán, Purpus 8460 (GH, MICH, MO, NY, UC, US); Barranca del Fortín, Purpus 16579 (US).

DOMINICAN REPUBLIC. Cordillera Central, Monte Cristi, Monción, Arr. La Majagua, Ekman 13063 (BM, G, NY, US).

Discussion. Of the other three varieties of A. tomentosa, var. mexicana resembles var. anthriscifolia most closely on the basis of its dissection, spores and stomates large, texture occasionally subcoriaceous, and the position of the fertile pinnae frequently approximate to the sterile pinnae. It differs markedly from var. anthriscifolia, however, in its yellow stipe, the linear-oblong shape of the subbasally attached unicellular trichomes, in having marginal spicules lacking, and in having sexual reproduction.

Like var. anthriscifolia, var. mexicana is a hexaploid, and therefore probably had the same general type of origin, i.e., by hybridization of a tetraploid and a diploid. However, in this variety the plant is a sexual polyploid.

I have included in this variety specimens from Haiti and Colombia which resemble somewhat the unusual specimens from Bolivia in their small spores and stomates and the ovate unicellular trichomes. These may be part of the same element.

34. Anemia ferruginea H.B.K.

Rhizome horizontal; hairs maroon to red; fronds caespitose; stipe 1.0-1.5 mm broad, usually dark purple, subglabrous to hirsute; blade deltoid to deltoid-ovate, bipinnate to bipinnate-pinnatifid, coriaceous; fertile pinnae approximate to the sterile pinnae, exceeding the sterile blade; spore ridges smooth, spongy-medullate; reproduction apogamous.

Most authors have treated A. ferruginea as distinct, but have given it the name A. fulva. On the basis of the locality, description and illustration of the type, Anemia fulva is, however, properly a synonym of A. tomentosa var. tomentosa. Anemia ferruginea differs from A. tomentosa chiefly by its coriaceous texture and red to maroon rhizome hairs.

The similarity in life cycle and the complementary geographical ranges of A. tomentosa and A. ferruginea immediately suggest a close relationship between them. Examination of their morphological features confirms this. The resemblance of A. ferruginea to A. tomentosa var. anthriscifolia is the most marked. They both have their fertile pinnae approximate to the sterile; their stipes are usually darkly pigmented (more consistently in A. ferruginea, however); the stipes are slender; the subbasally attached unicellular trichomes are short and ovate; the two species show the same variation in size, blade shape, and dissection.

The obvious question that poses itself is whether A. ferruginea might not best be treated as a variety of A. tomentosa. Within A. ferruginea, however, there are two very closely related varieties, and within A. tomentosa there are four varieties, which are more closely related to one another than to those of A. ferruginea. If these were all lumped into one species, their respective varieties would have to be considered as referable to two subspecies of species A. tomentosa. Not only is this unwieldy and inconvenient, but it would create a species much larger and more diverse than any other in the genus.

This treatment is tentative for there is much to be said on the side of interpreting A. tomentosa and A. ferruginea as one species. They are

very closely related to each other, compared to other species of the genus, and their ranges are generally allopatric, as shown in the combined map (Pl. IX, Fig. C).

34a. Anemia ferruginia H.B.K. var. ferruginea (Pl. XXX, Fig. A).
Anemia ferruginea H.B.K., Nov. Gen. et Sp. 1:32. 1815.
Anemia fulva β robusta Presl, Suppl. Tent. Pterid. 84. 1845.
Aneimia rubrostipes Pohl in Mart., Fl. Bras. 1(2):202. 1859.

Rhizome horizontal, 0.6-1.4 cm thick; hairs maroon to red-maroon; fronds caespitose; stipe terete, 4-36 cm long, 1-2 mm broad, usually dark purple, rarely yellow, pilose to hirsute; blade deltoid to deltoid-ovate, bipinnate to slightly bipinnate-pinnatifid, coriaceous, 5-20 cm long; pinnae 8-12 pairs; pinnules deltoid to elongate, obtuse, subglabrous to hirsute; the subbasally attached unicellular trichomes ovate; marginal spicules regularly present; fertile pinnae petiolate, erect, approximate to the sterile pinnae, far exceeding the sterile blade; spores 85-140 μ, tetrahedral-globose, frequently abortive and irregular, the angle protuberances conspicuous, the ridges smooth, spongy-medullate; reproduction apogamous.

Distribution. Southern Brazil and Bolivia, the Andes, northern South America, and Honduras (Pl. IX, Fig. C).

Type collection. "Prope Guardia de San Augustin, locis umbrosis, udis, altitudine 525 hexapodarum (Prov. Cumanenssi [Venezuela]), Humboldt and Bonpland." I have not seen the type, which is probably in the Humboldt Herbarium at P.

Selected specimens examined. BOLIVIA. LA PAZ: Apolo, Williams 1365 (GH, NY, UC, US); Yungas, Bang 438 (BM, MICH, MO, NY, UC, US).

BRAZIL. AMAZONAS: Rio Uraricuera, Serra de Xiriry, Luetzelburg 20756 (NY, R, UC). GOIAS: Region of the southern Serra Dourada, 16 km. e. of Formoso, Dawson 15115 (MICKEL, US). MATTO GROSSO: Cuyabá, Malme 3101 (US). MINAS GERAIS: S. Terezinha, Ituiutaba, Ereta do Resfriada, Macedo 2255 (BM, MO, US). PARANA: Morungava, Dusen 16480 (MO, NY, US). RIO DE JANEIRO: Itatiaya, Sampaio, no date (R no. 16062) (UC). SAO PAULO: Jundiahy, Brade 7609 (NY, S-PA, UC).

BRITISH GUIANA. Northwestern slopes of Kanuku Mountains, in drainage of Moku-moku Creek, A.C. Smith 3392 (F, MO, NY, S-PA, US); Mt. Roraima, Ireng Valley, Quelch and McConnell 201 (K).

COLOMBIA. ANTIOQUIA: Copacabana, Henri-Stanislas 1677 (US). CAUCA: Alto San Francisco, André 2860 (F, K, NY, US). CUNDINAMARCA: Cerro de Avila, André 1709 (K). HUILA: San Antonio Fortalecillas, Fosberg 19716 (US). MAGDALENA: Santa Marta, Jiracasaca, H.H. Smith 1109 (BM, BR, F, GH, K, MO, NY, S-PA, US). SANTANDER: Río Suratá valley, near Bucaramanga, Killip and A.C. Smith 16201 (BM, NY, US). TOLIMA: Cundai, Lehmann 2547 (BM, US). VALLE DEL CAUCA: Río Cali in vic. of Cali, Ewan 15970 (US).

ECUADOR. El Oro, near junction of Río Luis and Río Ambocas, 10 km. due s. of Portovelo, Wiggins 10, 916 (NY).

HONDURAS. Morazán, drainage of the Río Yeguare, hills near Las Mesas, Williams 17238 (F).

PERU. APURIMAC: Grau, Kairanca, Vargas 5864 (UC). CUZCO: Bajada de Pavayoc Vilcanota R., Bues 993 (US). SAN MARTIN: Prope Tarapoto, Spruce 4044 (BM, BR, G, P, NY, US). VILCABAMBA: Torontoy, Herrera 1308 (US).

VENEZUELA. AMAZONAS: Pto. Ayacucho, Williams 15936 (US). ARAGUA: prope coloniam Tovar, Fendler 7 (BR, G, GH, MO, US). BOLIVAR: rocky slopes between Ciudad Bolivar and Río Caroní, Steyermark 57595 (GH, MO, US). CARABOBO: Hacienca de Cura, near San Joaquín, Rincón del Diablo, Pittier 7974 (GH, US). DISTRITO FEDERAL: Caracas, Linden 180 (K). SUCRE: Cumaná, Guanaguana, Sa. de Cumaná, Funck 197 (BM, BR, G, K). TRUJILLO: near Escuque in savannas on road to Valera, Pittier 13146 (MO, NY, US).

Discussion. This is by far the most common and widespread of the two varieties. It ranges all the way from Brazil to Honduras. Its characters are fairly uniform in western South America and Brazil, but in Venezuela the leaves are often more dissected, more pubescent, and with stipes less strongly pigmented. The original description applies most closely to the latter form, as the type was collected in the vicinity of Cumaná, Venezuela.

34b. Anemia ferruginea H.B.K var. ahenobarba (Christ) Mickel, comb. nov. (Pl. XXX, Fig. B).

Aneimia ahenobarba Christ in Schwacke, Pl. Nov. Mineiras 2:37. 1900.

Anemia tripinnata Copeland, Univ. Calif. Publ. Bot. 17:24 t. 1. 1932.

Hemianemia ahenobarba (Christ) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Hemianemia tripinnata (Copeland) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Rhizome horizontal, 0.8-1.5 cm thick; hairs maroon; fronds caespitose; stipe terete, 6-34 cm long, 1-2 mm broad, dark purple, pilose to hirsute; blade deltoid, bipinnate-pinnatifid, coriaceous, 5-16 cm long; pinnae 10-17 pairs; pinnules lanceolate, acute or acuminate, pilose to hirsute; the subbasally attached unicellular trichomes ovate; marginal spicules regularly present; fertile pinnae petiolate, erect, approximate to the sterile pinnae, far exceeding the sterile blade; spores 88-130 μ, tetrahedral-globose, frequently abortive and irregular, the ridges smooth, spongy-medullate; reproduction probably apogamous.

Distribution. Southeastern Brazil (Pl. IX, Fig. C).

Type collection. "Goyaz [Brazil], montagnes, copiose, Ule 584, 3203." I have seen neither specimen, and therefore have no basis for designating a lectotype. The syntypes are probably in the Christ collection at P.

Selected specimens examined. BRAZIL. BAHIA: Jacobine, Blanchet, no date (G p.p.). GOIAS: 3 km. w. of Formoso at the foot of the Serra Dourada (e. of Amaro Leite), Dawson 1511 (US); near the capital, Ule 534 [= 584?] (R, UC, isotypes?); Jataí, Ribeirão Grande, Macedo 2172 (MO, RB, US); Serra de Natividade, Gardner 3559 (K). MATTO GROSSO: H. Smith 155 (R). MINAS GERAIS: arredores de Bello Horizonte, Campos Porto and Sagundes 2187 (BM, MICH); Serra do Cipó (110 km. n.e. of

Bello Horizonte), Chase 9254½ (US); Serra do Curral, s.e. of Bello Horizonte, Chase 9061 (US); Ronte de Caethé, pres de la mine d'or de Cuyaba, Damazio 985 (P); Caldas, Hosén 4646 (S-PA); Corinto, Fazenda do Diamante, base of Serra de Anjico, Mexia 5627 (F, GH, K, MICH, MO, NY, UC); Hercuilio Alves Acude, Duarte 1060 (RB); Ituiutaba, Aroeira, Macedo 2334 (RB, US); Serra do Ouro Branco, Metallurgica, Chase 10300 (GH, US); Ouro Preto, Badini 186 (RB); Patos de Minas, Cascata, Duarte 3046 (RB); Ressaguinha, Duarte 748 (RB); Rio das Pedras, Claussen 75 (BR, FI, US); Sabara, Damazio 2 (P); São Sebastião de Paraíso, Fazenda de Bocaina, proximo M. de Guayanazes, Vidal I-415 (R); Sta. Lucia, Rio das Velhas, Schwacke 11448 (RB).

Discussion: Variety ahenobarba is distinguished from var. ferruginea by its greater dissection and more acute to acuminate pinnule shape. Although I have no gametophytes of this variety, the irregular spore production strongly suggests that it is apogamous, as is var. ferruginea. The two varieties are often difficult to distinguish in a number of apparently intermediate specimens. If both varieties are really apogamous, then it would be possible for them to exist sympatrically and maintain their identities. The intermediate specimens may be due to their natural range of variation, but on the other hand, if occasional sexual populations exist, they could allow the two to introgress to some extent.

This dissected variety of A. ferruginea may be nearly indistinguishable from the form of A. tomentosa var. anthriscifolia in Bahia, Brazil, but the specific differences of A. ferruginea from A. tomentosa, i.e., the red to maroon rhizome hairs, coriaceous texture, and marginal spicules, do hold.

35. Anemia myriophylla Christ, Bull. Herb. Boiss. II. 7:793. 1907. (Pl. XXI, Fig. A).
Hemianemia myriophylla (Christ) Reed, Bol. Soc. Brot. II. 21:157. 1948.

Rhizome horizontal, 0.7-1.3 cm thick; hairs red; fronds scattered; stipe terete, 4-16 cm long, 1-2 mm broad, yellow, lanose; blade deltoid-ovate, bipinnate-pinnatifid, chartaceous to subcoriaceous, 4-14 cm long; pinnae 7-13 pairs; pinnules oblong, segments obdeltoid, lanose, especially on the abaxial surface; fertile pinnae petiolate, erect, subapproximate to the sterile pinnae, about the same length as the sterile blade; spores 78-94 μ, tetrahedral-globose, the angle protuberances conspicuous, the ridges subverruculate, spongy-medullate.

Distribution. Bolivia (Pl. IX, Fig. D).

Type collection. "Bolivia austr., Padcaya, 2100 m., 10, 12, 1903. K. Fiebrig 2541." I have not seen the type which is probably in the Christ collection at P. (P!, presumably an isotype).

Specimens examined. ARGENTINA. STATE UNKNOWN: La Laguna, d'Orbigny 413 (BR, F, G).

BOLIVIA. CHUQUISACA: Cerro Macho, Sucre, Cárdenas 496 (GH); Cinti, Weddel 3919 (P). COCHABAMBA: Calera, Santivañez, Jansson 3 (S-PA); about 5 km. s.e. of Cochabamba, Eyerdam 24094 (UC). SANTA CRUZ: Sarna pata, Steinbach 8552 (K). TARIJA: Padcaya, Fiebrig 2541 (P); Rincón de la Victoria, 16 km. s.w. of Tarija, West 8320 (MO, UC).

STATE UNKNOWN: Bolivian Plateau, Bang 1093 (BM, GH, MO, NY, US); Teneria, Herzog 1554 (UC), Herzog 2497 (US); Bridges, no date (BM).

CHILE. Ex herb. Limming (BR).

Discussion. The most outstanding characteristics of Anemia myriophylla are the fine dissection and heavy indument. It has several characters of the A. tomentosa-ferruginea complex, such as subverruculate spore ridges with a conspicuous spongy medulla, fertile pinna origin subapproximate to the sterile pinnae, and geographical range, and it shares distinctive characters of A. ferruginea (red rhizome hairs) and A. tomentosa (scattered petiole bases). It is apparently an offshoot of this complex, arising either from an intermediate ancestor or from hybridization between the two.

36. Anemia karwinskyana (Presl) Prantl, Schiz. 99. 1881 (Pl. XXXI, Fig. B)

Aneimia villosa ζ ? karwinskyana Presl, Suppl. Tent. Pterid. 83. 1845.

Anemia rosei Maxon, N. Am. Fl. 16:46. 1909.

Hemianemia karwinskyana (Presl) Reed, Bol. Soc. Brot. II. 21:162. 1948.

Hemianemia rosei (Maxon) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Rhizome horizontal, 1.0-1.5 cm thick; hairs orange; fronds caespitose; stipe terete, 6-33 cm long, 1.0-3.5 mm broad, yellow, pilose to hirsute; blade deltoid-ovate, bipinnate, rarely bipinnate-pinnatafid, subcoriaceous, 8-16 cm long; pinnae 8-12 pairs, mostly catadromous; pinnules narrowly adnate, subcordate at base, ovate-obtuse, lobes rounded, hirsute; fertile pinnae petiolate, erect, remote from the sterile pinnae, shorter than or equal to the sterile blade; spores 78-101 μ, tetrahedral-globose, the angle projections inconspicuous or lacking, the ridges subverruculate, spongy-medullate; chromosomes n = 76.

Distribution. Western Mexico (Pl. IX, Fig. A).

Type collection. Mexico, "Cristo, Karwinsky 8." I have not seen the type, which is probably in the Presl herbarium at PRC. (US!, isotype).

Specimens examined. MEXICO. GUERRERO: along main road about 10 mi. n. of Taxco, Degener 26, 282 (US); 1 mi. n. Agua del Obispo, Gray and Rowell 3007 (US); Acapulco, Sierra Madre, Providencia, Hancock 36 (K); Montes de Oca, Vallecitos, Hinton 11338 (BR, F, G, MO, NY, US); Achotla, trail w. of Suriana, Sierra Madre del Sur, n. of Río Balsas, Mexia 8804a (UC); Cuernavaca, Iguala-Taxco, Reiche, in Oct. 1926 (UC); 25 mi. s. of Chilpancingo, Rowell and Barkley 17M811 (BM); Storer 108 (US); Real de Guadalupe, Langlassé 353 (US). JALISCO: near Guadalajara, vicinity of Río Blanco, Rose 7500 (NY, US); Sierra de San Estéban, Pringle 11254 (F, MO, NY, US). MEXICO: Amatepec y cercanias, Matuda 29856 (US); Cerro de la Culebra, Luvianos, Progreso, Matuda 31466 (US); Temascaltepec, Real de Ariba, Hinton 12 (G, K); Temascaltepec, Hinton 2077 (K, MO, NY, US); Temascaltepec, Penon, Hinton 2141 (K, MO, NY, US), Hinton 2683 (K, US), Hinton 7347 (F, G, GH, K, NY, US). OAXACA: Cercanias de Tepenixtlahuaca, Conzatti 4369 (US). STATE UNKNOWN: prope Cristo, Karwinsky, in 1827 (US, isotype); Karwinsky [?] (FI).

Discussion. There is probably polyploidy within Anemia karwinskyana. Most specimens have a stomate length of about 45 μ, but in one collection ca. 57 μ.

Along with Anemia guatemalensis and A. colimensis, A. karwinskyana forms a distinct and closely knit group which has apparently diverged from the A. tomentosa complex. It has in common with this group the orange horizontal rhizome, fertile pinna origin remote from the sterile pinnae, and spore ridges which are somewhat verruculate and spongy-medullate.

The A. karwinskyana group of species is distinguished by its narrow pinnule bases, rounded segment lobes, yellow stipe, catadromous pinnae, and spores with rounded angles.

37. Anemia guatemalensis Maxon, N. Am. Fl. 16:46. 1909. (Pl. XXXII, Fig. A).
Hemianemia guatemalensis (Maxon) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Rhizome horizontal, 1.0-1.5 cm thick; hairs orange; fronds caespitose; stipe terete, 9-41 cm long, 1-2 mm broad, yellow, pilose to hirsute; blade deltoid-ovate, bipinnate-pinnatifid to tripinnate, subcoriaceous, 7-25 cm long; pinnae 9-14 pairs, mostly catadromous; pinnules and segments narrowly adnate, ovate to lanceolate with ovate lobes, pilose; fertile pinnae petiolate, erect, remote from the sterile pinnae, shorter than the sterile blade; spores 75-101 μ, tetrahedral-globose, the angle protuberances lacking, the ridges subverruculate, spongy-medullate.

Distribution. Guatemala, Honduras and El Salvador (Pl. IX, Fig. A).

Type collection. Guatemala, Dept. of Santa Rosa, Cerro Gordo, altitude about 1050 meters, August 1892, Heyde and Lux, distributed by Captain John Donnell Smith under no. 4095. Maxon reports that the type is at US. (US no. 830301!,type; GH!, MO!, NY!).

Selected specimens examined. GUATEMALA. BAJA VERAPAZ: Ormud Salamá, Cook 268 (US). CHIMALTENANGO: along road from Chimaltenango to San Martín Jilotepeque, Standley 57924 (F, MICH, US). CHIQUIMULA: Alotepeque, Tejada 230 (US). ESCUINTLA: Texcuaco, Morales 1.072 (F). GUAJINIQUILAPA: Sta. Rosa, Lehmann 1714 (BM). GUATEMALA: Cerca de Guatemala, Río de las Vacas, Tonduz 854 (BM, F, G, K, NY, US). HUEHUETENANGO: Aguacatan road, 10 km. e. of Huehuetanango, Standley 82093 (G, US). JALAPA: 8 km. n. of Jalapa, Cutler 4321 (MO, US). QUICHE: Aguilar 1440 (F). SANTA ROSA: Cerro Gordo, Heyde and Lux 4095 (US, type; GH, MO, NY, US).

HONDURAS. COMAYAGUA: Vicinity of Siguatepeque, Standley 55836 (F, US). EL PARAISO: 2 km. n.w. of Guinope, near Manzaragua road, Standley 17256 (F). FRANCISCO MORAZAN: region of Agua Amarilla, above El Zamorano, Standley and Williams 453 (F).

EL SALVADOR. Hda. San José n. Metapán, Rep. Sta. Ana, Rohweder no. El Salvador 2665 (BM).

Discussion. The greater dissection, lanceolate pinnules and geographical range distinguish Anemia guatemalensis from A. karwinskyana, but in other respects the two are nearly identical. Perhaps future research will justify placing them as geographically isolated varieties of a single species.

38. Anemia colimensis Mickel, sp. nov. (Pl. XXXII, Fig. B).

Rhizomate erecto, ca. 1 cm crasso; pilis castaneis; foliis caespitosis; petiolo tereti, 8-14 cm longo, ca. 1 mm lato, stramineo, atrobrunneo ad basis, piloso vel hirsuto; lamina deltoido-ovata, tripinnata vel tripinnata-pinnatifida, subcoriacea, 7-17 cm longa; pinnis 11-14 = jugis, plurimis catadromis; pinnulis nunc brevi-petiolatis nunc anguste adnatis, venis hirsutis cum pilis multicellularibus in superficie abaxiali, superficie adaxiali cum pilis magnis, rigidis, unicellularibus. Pinnas fertiles sporasque non vidi.

Distribution. Known only from the type collection (Pl. IX, Fig. A).

Type: Mexico, Colima, mountains 10 miles south-southwest of Colima on Manzanillo road, elev. 400-500 m., 18 July 1958, R. McVaugh 15537.

Specimens examined. MEXICO. COLIMA: Mts. 10 mi. ssw of Colima on Manzanillo Road, McVaugh 15537 (MICH, type).

Discussion. The fine dissection of this new species readily sets it apart from the closely related A. karwinskyana and A. guatemalensis. It is further peculiar in its upright rhizome, dark rhizome hairs, dark stipe bases, and large unicellular hairs. These characters, together with the uniformity of the several plants of the collection, seem to justify the description of a new species, in spite of the fact that fertile material is yet unknown.

HYBRIDS

1. Anemia ferruginea var. ferruginea X flexuosa.

Distribution. Bolivia.

Specimens examined. BOLIVIA. LA PAZ: Nordyungas, Milluguaya, Buchtien 794 (F, G p.p., BM, K, NY p.p., S-PA, US).

Discussion. This putative hybrid was found growing with the two presumed parents, and has abortive spores. It resembles A. ferruginea in its fertile pinnae that exceed the sterile blade in height, and in its stipe which is at least partially dark-pigmented. Relationship with A. flexuosa is seen in the fertile pinna position remote from the sterile and the stipes mostly yellow. Dissection and rhizome color is intermediate between the two species.

These two species have been collected together at other times in Bolivia and Peru, and it is perhaps surprising that more hybrids between the two have not been found.

2. Anemia ferruginea var. ferruginea X villosa

Distribution. Colombia.

Specimens examined. COLOMBIA. CAUCA: Lehmann 4418a (K); Lehmann 4419 (US).

Discussion. Although the ranges of the two parents overlap in Brazil and much of northern South America, the only hybrids found between them have been in Colombia. The putative hybrid is distinctive in its elongate-deltoid frond shape and fertile pinna position subapproximate to the sterile pinnae, both characters intermediate between the two probable parents. In dense hairiness and stout stipe it resembles A. villosa, while in marginal spicules, coriaceous texture, and long fertile pinnae it resembles A. ferruginea. The spores are abortive.

3. Anemia myriophylla X tomentosa var. anthriscifolia

Distribution. Bolivia.

Specimens examined. BOLIVIA. COCHABAMBA: Calera, Santivañez, Janson 5 (S-PA).

Discussion. Its complete spore abortion and intermediate dissection suggest a hybrid origin of this plant although additional distinctive characters are few. It was collected at a high elevation where A. myriophylla is found, and the abundant lightly pigmented hairs and suggestion of bipinnate-pinnatifid dissection shows that that species is involved. For the most part, however, it is only bipinnate, one leaf being deeply bipinnate-pinnatifid, and the rhizome hairs are a reddish orange. An odd form of A. tomentosa of Bolivia, which I have referred to var. anthriscifolia, is probably the other parent. The only other possible parent would be A. flexuosa, which is much larger and more distantly related.

4. Anemia imbricata X villosa

Distribution. Minas Gerais, Brazil.

Specimens examined. BRAZIL. MINAS GERAIS: Damazio 1381 (NY).

Discussion. The extremely close relationship of the two putative parents often makes them difficult to distinguish. The hybrid has abortive spores, is intermediate in pubescence and breadth of the blade, and was growing with the two parents.

5. Anemia organensis X villosa

Distribution. Rio de Janeiro, Brazil.

Specimens examined. BRAZIL. RIO DE JANEIRO: Nova Friburgo-direcão de Duas Pedras-"Valvera," Lutz 1333 (BM, R); Nova Friburgo, Leite 1128 (F); Pedra Lisa, Santos Luis Junior 62 (R); Sta. Maria Magdalena, Serra da Turquilha, Santos Lima and Brade 14335 (RB); Sto. Antonio de Imbé, Brade and Santos Lima 11651 (R p.p., RB).

Discussion. The pinnae of this hybrid are shallowly pinnatifid, a condition intermediate between the simple pinnae of A. organensis and the pinnatifid pinnae of A. villosa. The relative position of the fertile pinnae in respect to the sterile pinnae varies from remote to approximate. The spores are abortive.

6. Anemia raddiana X villosa

Distribution. The states of Rio de Janeiro, Minas Gerais, and São Paulo, Brazil.

Specimens examined. BRAZIL. MINAS GERAIS: Caldas, Regnell III 1480 (US); Carandae-Quebracambão, Duarte 897 (RB); Damazio 18 (G, MICH).

RIO DE JANEIRO: Claussen 179?, in 1842 (BM, NY p.p.).

SAO PAULO: São J. do Barreiro, Hoehne and Gehrt 17658 (NY); Sebastianópolis, Martius, in 1848 (GH).

STATE UNKNOWN: Capanema 6702 (RB).

Discussion. This hybrid resembles A. raddiana in its broad blade and its slender fertile pinnae which exceed the sterile blade. On the other hand, it is similar to A. villosa, its frond being elongate and hirsute to tomentose. The spores are abortive.

7. Anemia imbricata X raddiana

Distribution. Minas Gerais, Brazil.

Specimens examined. BRAZIL. MINAS: Serra do Curral, prope Bello Horizonte, Silveira 114 (R p.p.).

Discussion. This presumed hybrid was found mixed in a single large collection including A. raddiana and A. imbricata. It has largely abortive spores, and in other respects closely resembles the hybrid A. raddiana X villosa. This is quite reasonable in light of the close relationship between A. imbricata and A. villosa.

8. Anemia X ulbrichtii Rosenstock, Festschr. Alb. v. Bamberg 66 t. 2. 1905.
Anemia spannagelii Rosenstock, Hedwigia 46:160. 1907.
Anemia grossilobata Christ, Denkschr. Akad. Wien 79:52. f. 1-2. t. 7 f. 2. 1907.

Distribution. In southern Brazil from Rio Grande do Sul to São Paulo.

Type collections: Two specimens are cited with the original description of A. X ulbrichtii: "São Paulo: Sandiger Wegabhang bei Toledo, 20 Marz 1903, A. Ulbricht 30; Rio Grande do Sul: In der Hähe der Rettungspikade im Munizipium Sta. Cruz, 6 November 1903, C. Juergens [134]." Because the plant was named for Ulbricht, I am designating Ulbricht 30 as the lectotype. The type is probably in the Rosenstock collection at S-PA. (NY!, S-PA!, UC!, isotypes).

Specimens examined. BRAZIL. RIO GRANDE DO SUL: Rio Pardo, Linna Allema, Jurgens (Rosenstock no. 337) (K, P, US); S. Cruz, Rettungspikade, Jurgens 134 (S-PA, UC).

SANTA CATARINA: Brusque, Spannagel 329 (HBR, UC); Enseada do

Brito, Spannagel 358 (HBR); Itacorobi, Rohr 297a (HBR, US); Lages Spannagel 79 (HBR, NY, UC), Spannagel 79a (S-PA), Spannagel (Rosenstock 412) (P).

SAO PAULO: Toledo, Ulbricht 30 (NY, S-PA, UC, isotypes); Campinas, Heiner 30 (S-PA p.p.); Sa. da Cantareira, Brade 6601 (UC); Ypiranga, Luederwaldt 7648 (NY); Horto Botanico do Museu Paulista, Sampaio 4300 (R).

STATE UNKNOWN: hort. Berol., Otto (BM); Barclay, in 1836 (BM); Linden 154 (BR); Usteri 33 (P).

Discussion. This is the only intersubgeneric hybrid as yet known. It is a cross between Anemia (subg. Coptophyllum) raddiana and A. (subg. Anemia) phyllitidis. The great morphological differences between the two parents have produced some interesting effects in the hybrid as reported by Rosenstock (1905) in his description in such characters as fertile pinna origin, dissection, venation, and stomatal position.

Taxa of Uncertain Status

1. Anemia pyrenea Taubert, Engl. Jahrb. 21:422. 1896.
   Hemianemia pyrenea (Taubert) Reed, Bol. Soc. Brot. II. 21:158. 1948.

I have seen only a photograph of a specimen at P. The plant is small with dimorphic fronds, as in A. millefolia and A. buniifolia. The sterile leaves closely resemble those of A. (subg. Anemia) heterodoxa.

2. Anemia tomentosa var. subsimplex Christ in Schwacke, Pl. Nov. Mineiras 2:37. 1900.
   Hemianemia tomentosa var. subsimplex (Christ) Reed, Bol. Soc. Brot. II. 21:161. 1948.

Christ claims this Brazilian plant is identical to one collected by Moritz at Tovar, Venezuela. From its range and from specimens collected by Moritz that I have seen, this may be a minute form of A. ferruginea or possibly A. villosa. On the other hand, Christ also says it most closely resembles A. (subg. Anemia) collina.

ACKNOWLEDGEMENTS

My deep appreciation is extended to Dr. Warren H. Wagner, Jr., of the University of Michigan for his encouragement and criticism throughout the course of this work. I am indebted to Mr. Conrad V. Morton of the United States National Herbarium for his invaluable advice and his aid in obtaining living specimens from Latin America. Mr. David B. Lellinger helped with the photography of specimens. I am grateful to the curators of the herbaria which lent me specimens and to the several people who sent me living plants of Anemia for my studies. I would like to thank also the many other persons who so kindly offered their criticism and assistance.

PLATE I

Internal Anatomy of *Anemia tomentosa* var. *mexicana* (Mickel 760)

Fig. A. Cross section of a root.

B. Cross section of petiole.

C. Longitudinal section of rhizome showing the axillary pockets.

D. Hairs lining the axillary pocket.

E. 1-5. Serial sections showing stelar development of a rhizome branch, beginning at bt in Fig. F_6.

F. 1-6. Serial sections of rhizome. ap = axillary pocket; lt = leaf trace; rt = root trace; sb = stelar bundle; bt = branch trace.

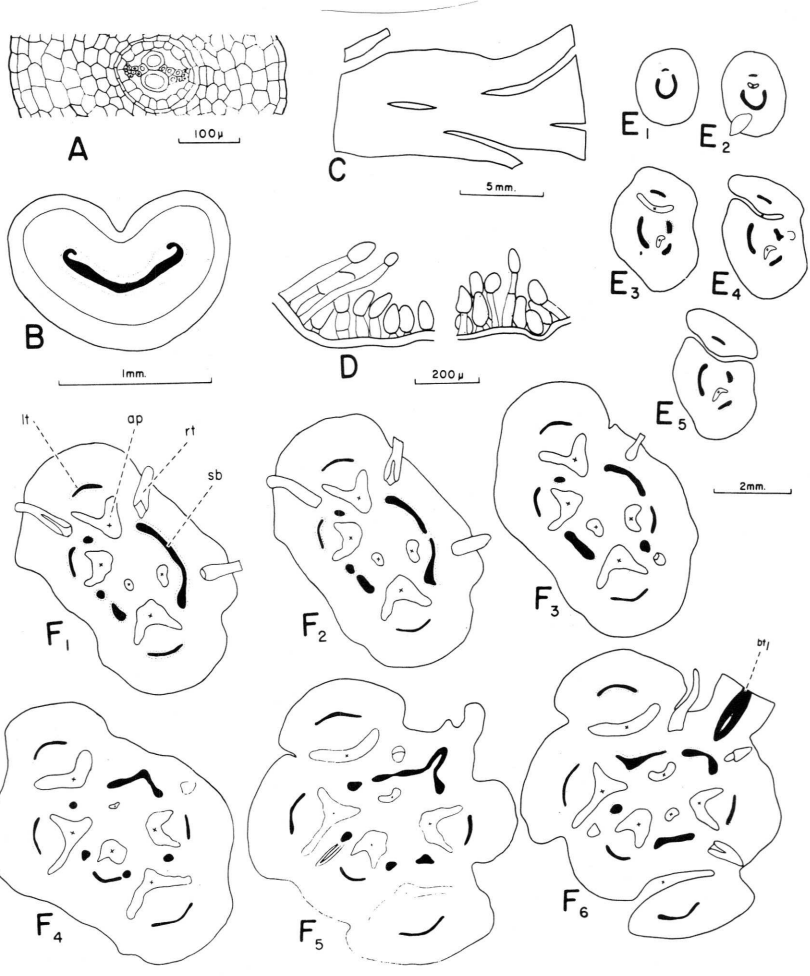

A
100μ
B
1mm.
C
5mm.
D
200μ
E1
E2
E3
E4
E5
2mm.
lt
ap
rt
sb
F1
F2
F3
F4
F5
F6
bt

PLATE II

Leaf Morphology in Anemia, subg. Coptophyllum

Fig. A. Medial pinnae.

1. A. flexuosa. Bang 304 (US).
2. A. karwinskyana. Hinton 7347 (GH).
3. A. ferruginea var. ferruginea. Williams 1365 (US).
4. A. ferruginea var. ahenobarba. Mexia 5627 (MO).

B. Leaf margin of Anemia ferruginea var. ferruginea. Bang 438 (UC).

C. Trichomes.

1. A. flexuosa. Williams 1364 (US).
2. A. smithii. Fosberg 19475 (US).
3. A. aspera. Brade 8560 (NY).
4. A. simplicior. Jorgensen 4065 (US).
5. A. ferruginea var. ferruginea. Bang 438 (UC).
6. A. smithii. Fosberg 19475 (US).
7. A. colimensis. McVaugh 15537 (MICH).

D. Venation patterns.

1. A. raddiana. Regnell 1480 (US).
2. A. X ulbrichtii. Jurgens 337 (US).
3. A. phyllitidis. Broadway 6728 (US).
4. A. aspera. Brade 8560 (NY).
5. A. blechnoides. Brade 19833 (RB).
6. A. lanuginosa. Damazio, Apr. 1907 (UC).

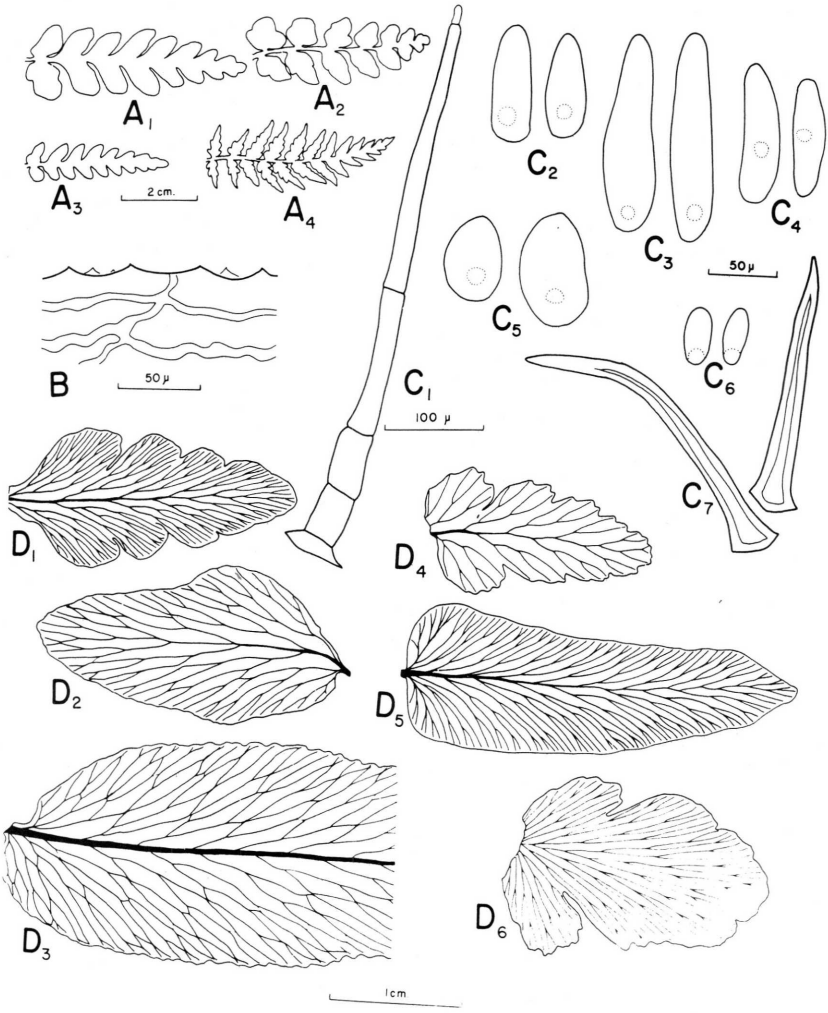

A1
A2
A3
2 cm.
A4
B
50 μ
C1
100 μ
C2
C3
C4
50 μ
C5
C6
C7
D1
D4
D2
D5
D3
D6
1 cm

PLATE III

Leaf morphology in Anemia, subg. Coptophyllum

Fig. A. Stomatal position.

1. Attached. A. tomentosa var. mexicana. Mickel 760.
2. Suspended. A. smithii. Fosberg 19475 (US).
3. Floating. A. smithii. Fosberg 19475 (US).

B. Epidermal cells.

1. A. tomentosa var. australis. Abbiotti 1043 (US).
2. A. gardneri. Brade 8583 (UC).
3. A. smithii. Fosberg 19475 (US).
4. A. bartlettii. Bartlett 11898 (UC).
5. A. elegans. Chase 9219½ (US).

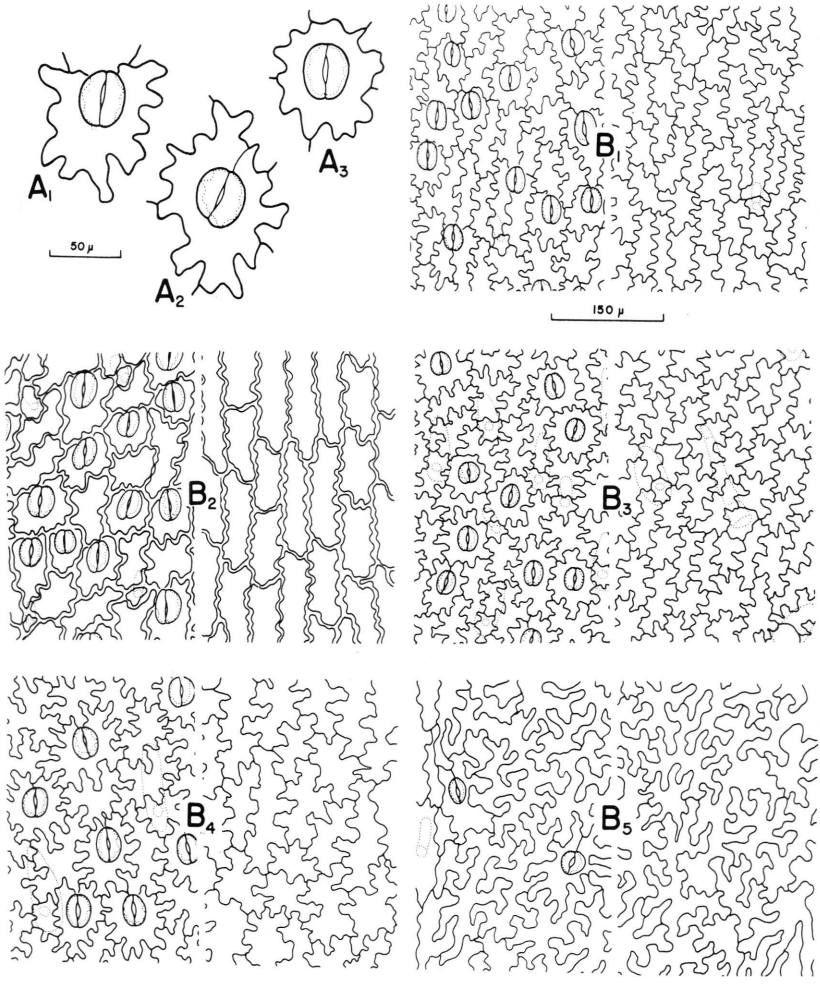

A1
A2
A3
50 μ
B1
150 μ
B2
B3
B4
B5

PLATE IV

Spores of *Anemia*, *Mohria* and *Ceratopteris*

Fig. A. 1-2. *Anemia tomentosa* var. *australis*

B. 1-2. *Ceratopteris thalictroides*

C. 1-2. *Mohria caffrorum*

D. 1-2. *Anemia adiantifolia*

E. 1-2. *Anemia phyllitidis*

F. *Anemia aspera*

G. *Anemia madagascariensis*

H. *Anemia karwinskyana*

I. *Anemia aethiopica*

J. *Anemia guatemalensis*

K. *Anemia flexuosa*

L. *Anemia lanuginosa* (outline)

M. *Anemia tomentosa* var. *anthriscifolia*

N. Spore ridges of *Anemia villosa*

1. Cross section; r = ridge, s = stria
2. Optical tangential section

O. Spore ridges of *Anemia tomentosa* var. *australis*

1. Cross section; m = medulla
2. Optical tangential section

P. Spore ridges of *Anemia adiantifolia*

1. Cross section
2. Optical tangential section

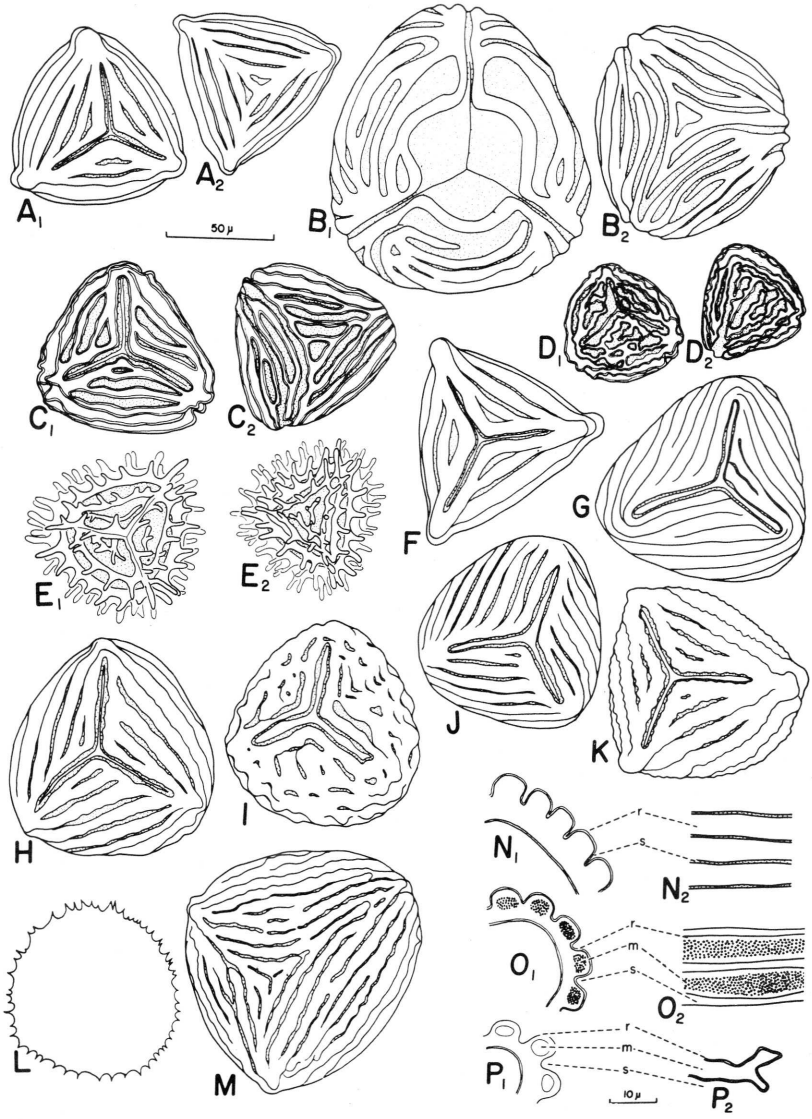

A1
A2
50 μ
B1
B2
C1
C2
D1
D2
E1
E2
F
G
H
I
J
K
L
M
N1
N2
O1
O2
P1
P2
r
s
m
10 μ

PLATE V

Gametophytes of Anemia tomentosa

Fig. A. 1-7. Early developmental stages in Anemia tomentosa var. anthriscifolia.

B. Cells from gametophyte of A. tomentosa var. anthriscifolia.

C. Trichome from gametophyte of A. tomentosa var. anthriscifolia.

D. 1-6. Mature gametophytes of A. tomentosa var. australis.

E. 1-6. Mature gametophytes and young apogamous sporophytes of A. tomentosa var. anthriscifolia.

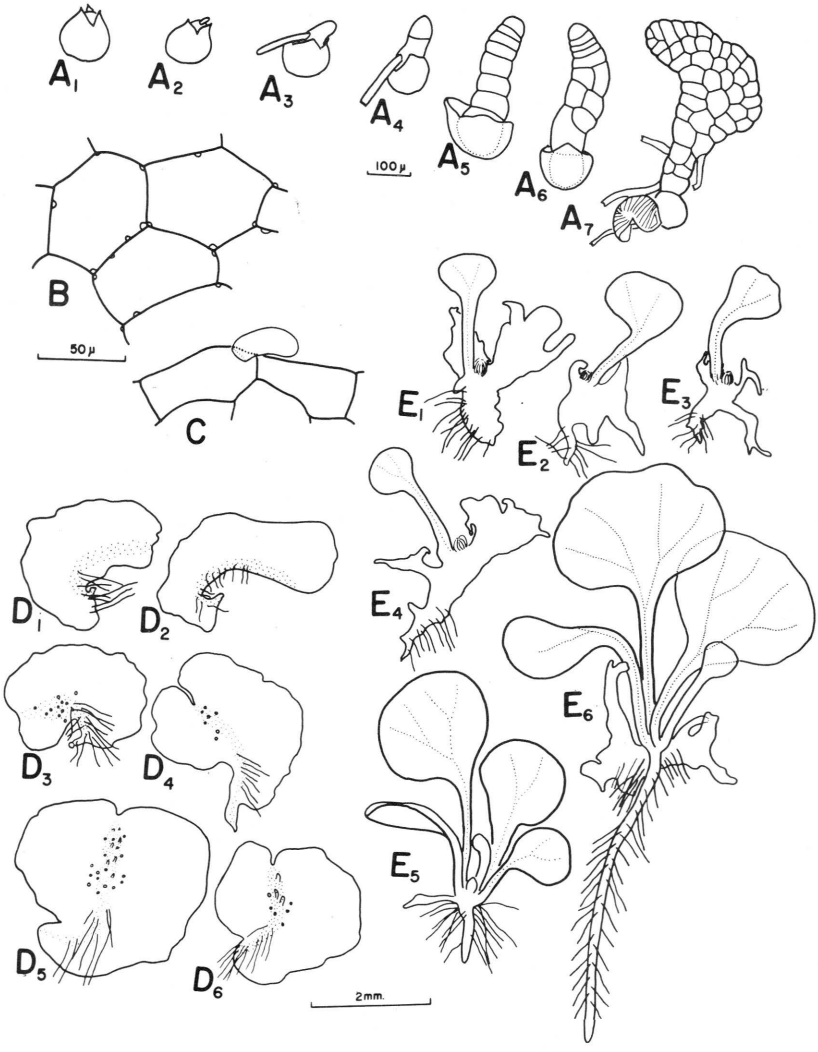

A1
A2
A3
A4
A5
A6
A7
100μ
B
50μ
C
E1
E2
E3
E4
E5
E6
D1
D2
D3
D4
D5
D6
2mm.

PLATE VI

Morphology and Chromosomes in Anemia and Mohria

Fig. A. Antheridium. Anemia tomentosa var. anthriscifolia.

1-3. Development.
4. Release of cap cell. c = cap cell.
5. Release of sperms.

B. 1-3. Archegonium. Anemia tomentosa var. mexicana.

C. Sporangia.

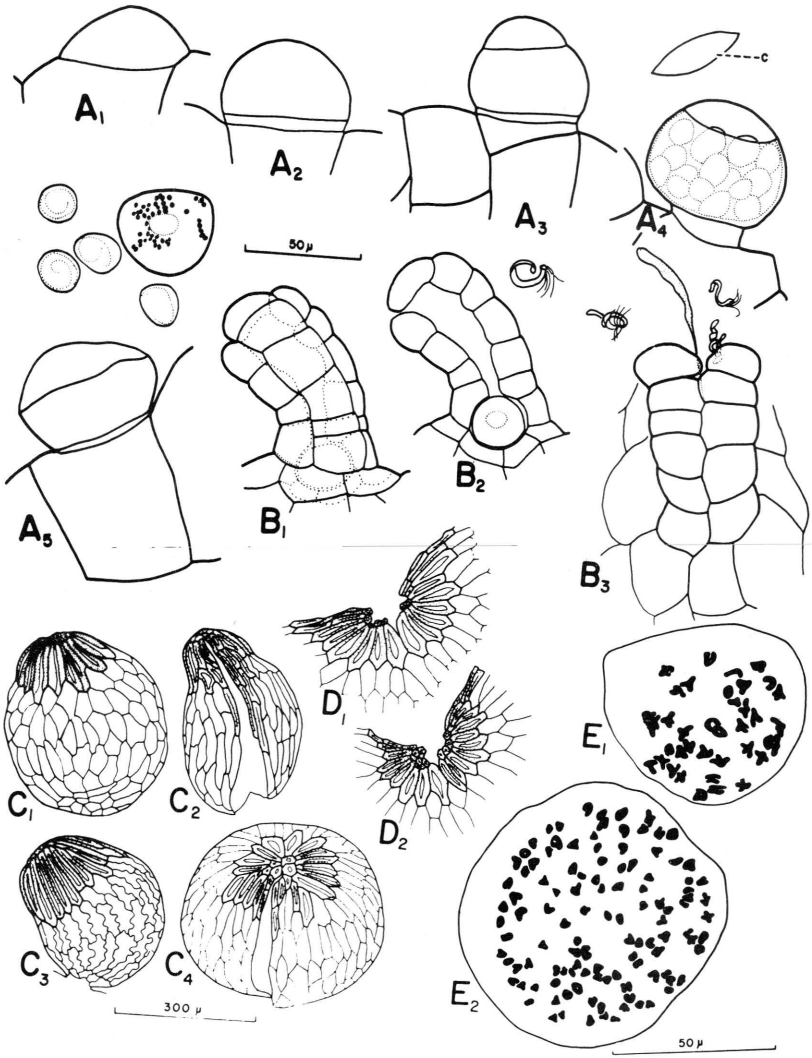
1. A. raddiana. L.B. Smith 1988 (GH).
2. A. pastinacaria. Seibert 536 (MO).
3. A. elegans. Maublanc 653 (F).
4. Mohria caffrorum. Mellen 1 (MICH).

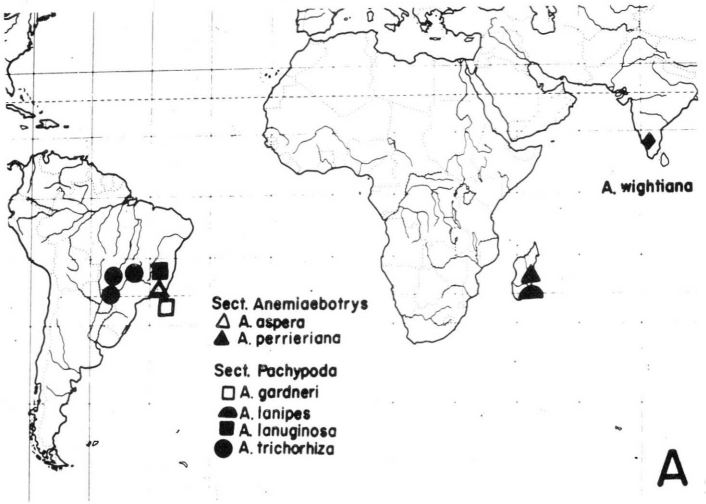
D. Annulus.

1. A. raddiana. L.B. Smith 1988 (GH).
2. A. madagascariensis. Humbert 2857 (GH).

E. Chromosomes.

1. A. adiantifolia. Jamaica, Proctor s.n. n = 38.
2. A. tomentosa var. anthriscifolia. Argentina, Córdoba, Sierra Chica, Lichtenstein s.n. n = 114.


A1
A2
A3
A4
c
50 μ
A5
B1
B2
B3
C1
C2
D1
D2
E1
C3
C4
300 μ
E2
50 μ



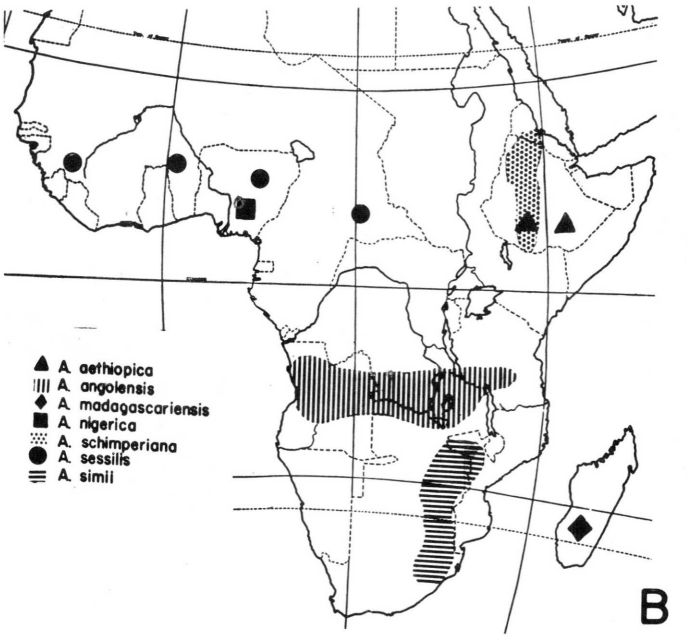


PLATE VII. Geographical Distribution of Anemia, subg. Coptophyllum

Fig. A. Section Anemiaebotrys, sect. Pachypoda, and Anemia (sect. Tomentosae) wightiana

B. Section Tomentosae: African species

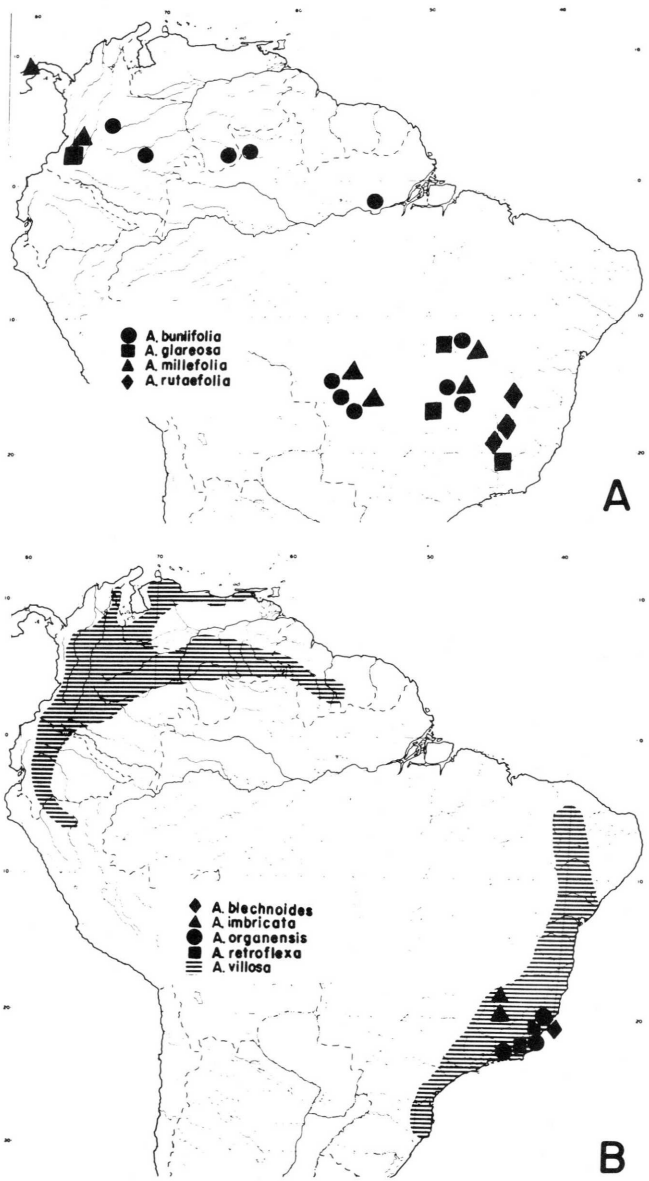


PLATE VIII. Geographical Distribution of Anemia, subg. Coptophyllum

Fig. A. Section Coptophyllum.

B. Section Tomentosae: Anemia blechnoides, A. imbricata, A. organensis, A. retroflexa, and A. villosa.

PLATE IX

Geographical Distribution of Anemia, subg. Coptophyllum

Fig. A. Section Tomentosae: Anemia bartlettii, A. colimensis, A. guatemalensis, and A. karwinskyana.

B. Section Adetostoma and sect. Trochopteris.

C. Section Tomentosae: Anemia ferruginea and A. tomentosa.

D. Section Tomentosae: Anemia flexuosa, A. myriophylla, A. raddiana, and A. simplicior.

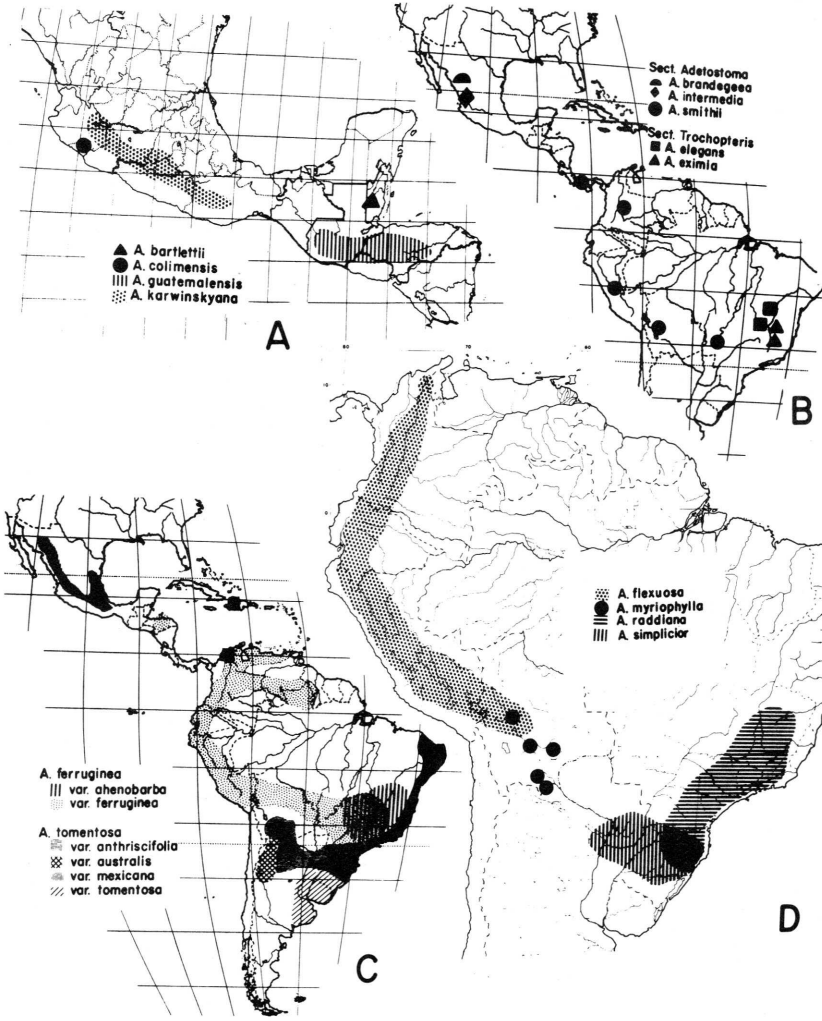

A. bartlettii
A. colimensis
A. guatemalensis
A. karwinskyana
A
Sect. Adetostoma
A. brandegeea
A. intermedia
A. smithii
Sect. Trochopteris
A. elegans
A. eximia
B
A. flexuosa
A. myriophylla
A. raddiana
A. simplicior
D
A. ferruginea
var. ahenobarba
var. ferruginea
A. tomentosa
var. anthriscifolia
var. australis
var. mexicana
var. tomentosa
C

PLATE X

Specializations in Mohria and the subgenera of Anemia

A. Rhizome compact (0) to creeping (1).

B. Rhizome lacking axillary pockets (0) to axillary pockets present (1).

C. Rhizome clothed with hairs (0) to scales (1).

D. Leaves polystichous (0) to distichous (1).

E. Fronds bipinnate to tripinnate (0) to simply pinnate (1).

F. Stomates attached (0) to suspended or floating (1).

G. Multicellular laminar hairs glandular (0) to nonglandular (1).

H. Sporangia borne on normal fronds and pinnae (0) to differentiated fertile pinnae or fronds (1).

I. Fertile pinnae held in same plane as sterile (0) to fertile pinnae held erect (1).

J. Insertion of fertile pinnae remote from sterile (0) to approximate (1).

K. Fertile pinnae with at least a remnant of lamina (0) to lacking any remnant of lamina (1).

L. Sporangia oval (0) to spherical (1).

M. Sporangial apical plate cells thick-walled (0) to thin-walled (1).

N. Spore ridges smooth (0) to clavulate (1).

O. Spore ridges broad (0) to narrow (1).

P. Spore ridges straight (0) to undulating (1).

Solid dots represent extant taxa; hollow dots represent hypothetical ancestral intermediates. The character letters are given the first time the advanced condition appears in an evolutionary line.

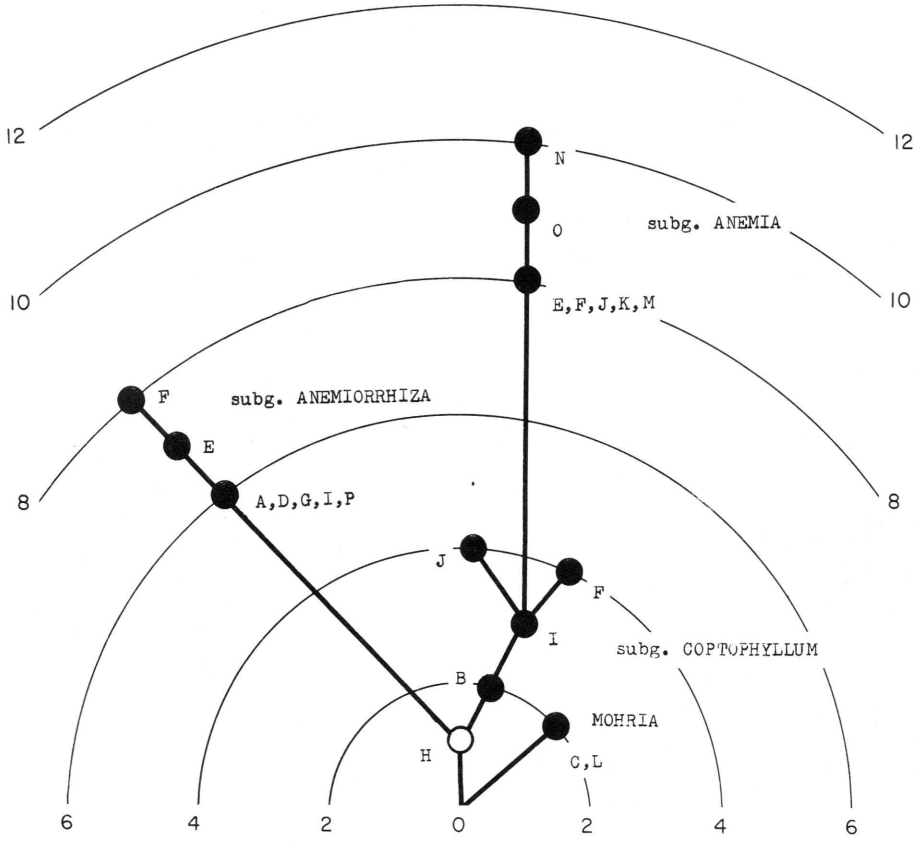

12
12
10
10
8
8
6
4
2
0
2
4
6
N
O
E,F,J,K,M
subg. ANEMIA
F
E
A,D,G,I,P
subg. ANEMIORRHIZA
J
F
I
B
H
C,L
MOHRIA
subg. COPTOPHYLLUM

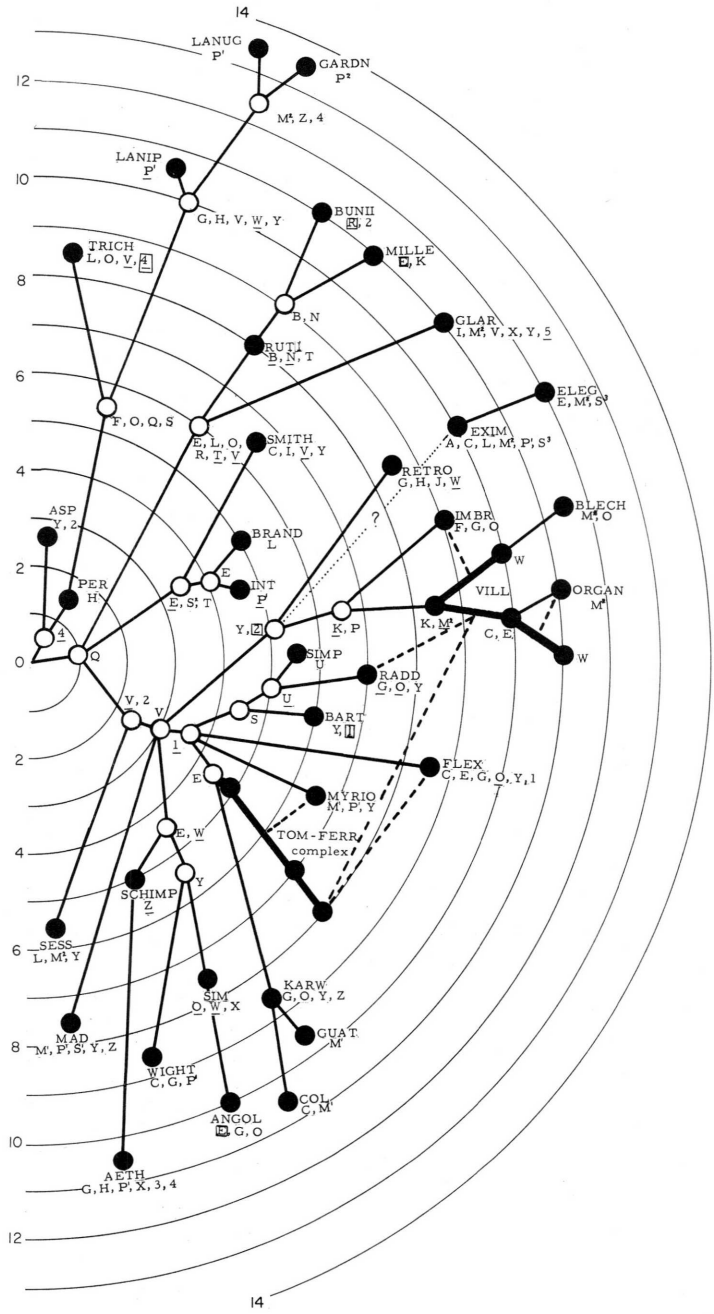
PLATE XI

Specializations in subgenus Coptophyllum

A. Leaves upright and spreading (0) to rosette-forming (1).
B. Fronds isomorphic (0) to dimorphic (1).
C. Rhizome horizontal (0) to oblique or erect (1).
D. Rhizome compact (0) to short-creeping (1).
E. Rhizome hairs maroon (0) to orange (1).
F. Rhizome hairs short, less than 1 cm (0) to long, ca. 1.5 cm (1).
G. Stipe 0.5-1.5 mm broad (0) to 2-3 mm broad (1).
H. Stipe approximately terete (0) to definitely flattened (1).
I. Stipe yellow to medium brown (0) to purple (1).
J. Rachis straight (0) to flexuous (1).
K. Blade outline deltoid-ovate (0) to linear-oblong (1).
L. Sterile fronds longer than 10 cm (0) to shorter than 10 cm (1).
M. Blade bipinnate or bipinnate-pinnatifid (0) to tripinnate (M^1) (1) or pinnate-pinnatifid (M^2) (1) to once pinnate (M^2) (1.5).
N. Lamina broad (0) to narrow (1).
O. Lamina chartaceous or membranous (0) to coriaceous (1).
P. Lamina pilose-hirsute (0) to lanose (P^1) (1) or glabrous (P^2) (1).
Q. Segments coarsely denticulate (0) to entire or serrate (1).
R. Margin lacking spicules (0) to spiculate (1).
S. Epidermal cell walls moderately lobed (0) to shallowly undulate (S^1) (1), or deeply lobed (S^3) (1) to sinuously lobed (S^3) (1.5).
T. Stomates affixed (0) to "floating" (1).
U. Attachments of large unicellular trichome subbasal (0) to medial (1).
V. Fertile pinnae horizontal (0) to erect (1).
W. Fertile pinnae remote from sterile (0) to approximate (1).
X. Fertile pinnae shorter than sterile blade (0) to exceeding sterile blade (1).
Y. Spore diameter less than 85 μ (0) to greater than 85 μ (1).
Z. Spore angle protuberances present (0) to absent (1).
1. Spore ridges smooth (0) to verruculate (1).
2. Spore ridges clear (0) to spongy-medullate (1).
3. Spore ridges parallel (0) to anastomosing (1).
4. Spore perine smooth (0) to spiculate (1).

Solid dots represent extant species; hollow dots represent hypothetical ancestral intermediates. The character letter or number is given the first time the specialized or divergent condition appears in an evolutionary line. Underlined letters represent intermediate conditions (value 0.5).

A square surrounding a letter signifies a reversion to the primitive condition. The dotted line indicates the most questionable relationship. Dashed lines represent hybridization, and the extra-heavy lines designate the species complexes of A. villosa and A. tomentosa-A. ferruginea.


14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
LANUG P'
GARDN P²
M¹, Z, 4
LANIP P'
G, H, V, W, Y
BUNII E, 2
MILLE E, K
TRICH L, O, V, 4
B, N
GLAR I, M¹, V, X, Y, 5
RUTI B, N, T
ELEG E, M¹, S²
F, O, Q, S
EXIM A, C, L, M¹, P', S'
E, L, O, R, T, V
SMITH C, I, V, Y
RETRO G, H, J, W
ASP Y, 2
BRAND L
IMBR F, G, O
BLECH M¹, O
W
PER H
E
INT P'
E, S', T
VILL
ORGAN M¹
Y, Z
K, P
K, M¹
C, E
4
Q
SIMP U
RADD G, O, Y
W
V, 2
V
U
S
BART Y, 1
1
FLEX C, E, G, O, Y, 1
E
MYRIO M', P', Y
E, W
TOM-FERR complex
SCHIMP Z
Y
SESS L, M', Y
SIM O, W, X
KARW G, O, Y, Z
MAD M', P', S', Y, Z
GUAT M'
WIGHT C, G, P'
COL C, M'
ANGOL E, G, O
AETH G, H, P', X, 3, 4

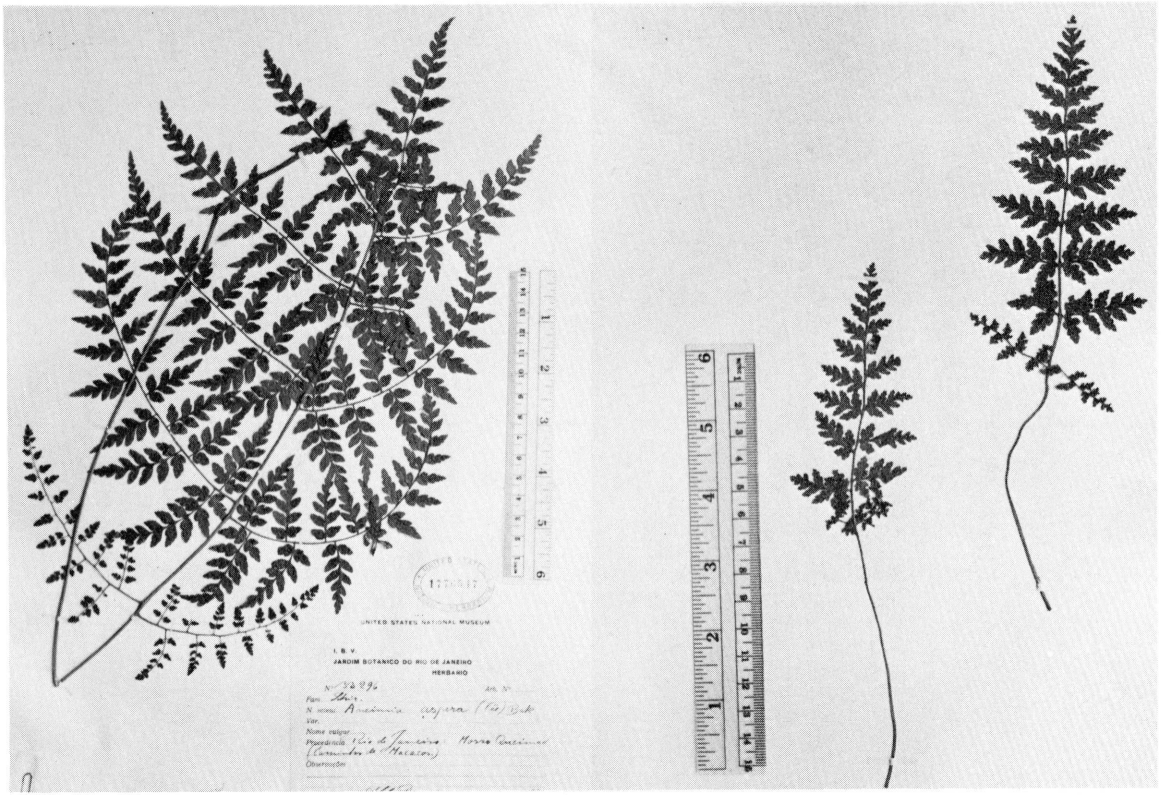


PLATE XII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia aspera. Brade 1933 (US). Fig. B. Anemia perrieriana. Perrier 7485 (BM, isotype).

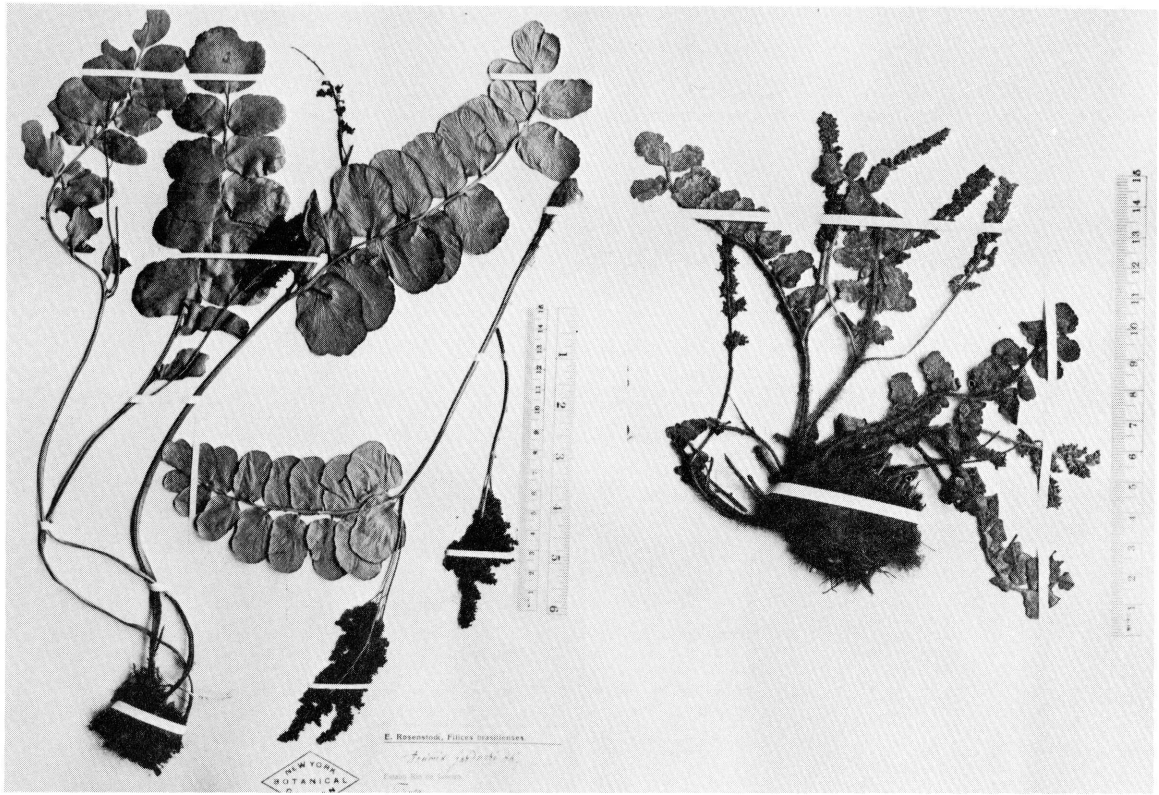


PLATE XIII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia gardneri. Brade 8583 (NY). Fig. B. Anemia lanuginosa. Damazio 1952 (NY).

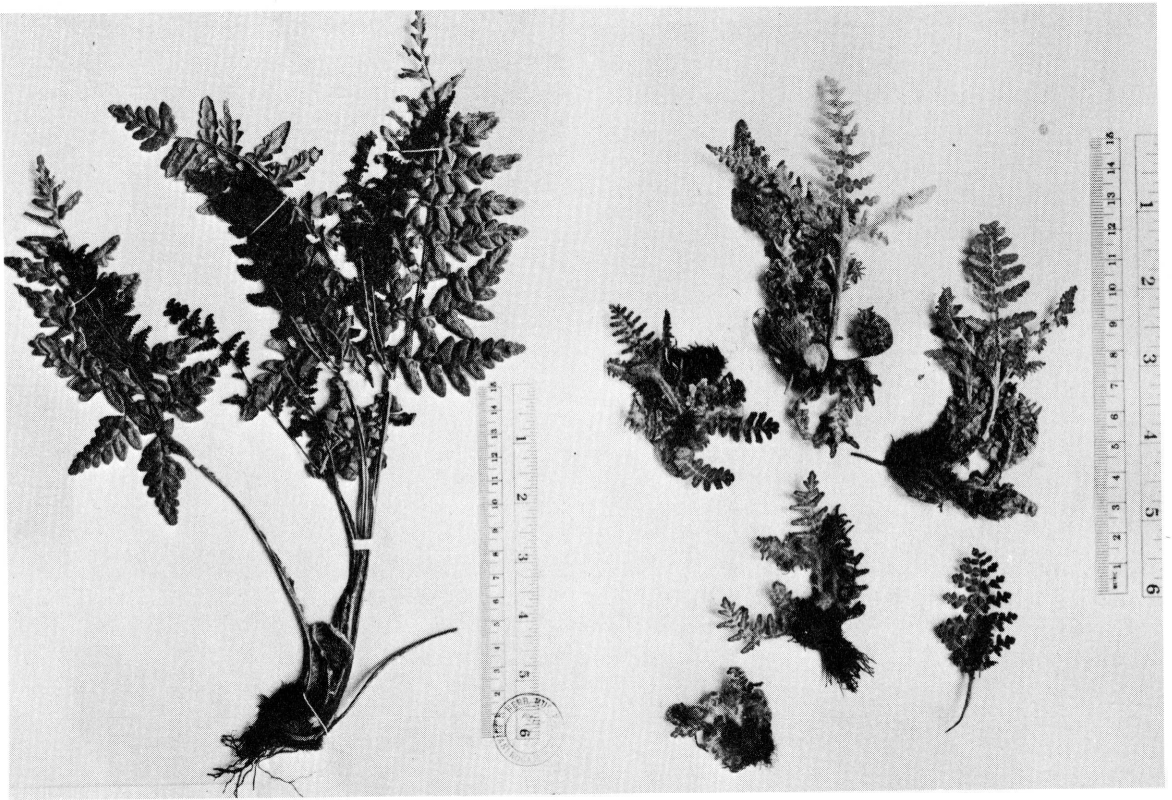


PLATE XIV. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia lanipes. Humbert 5808 (P, isotype). Fig. B. Anemia trichorrhiza. Ule 539 (R).

PLATE XV. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia buniifolia. Malme 3474a (US). Fig. B. Anemia millefolia. Lehmann 6400 (US).

PLATE XVI. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia rutifolia. Glaziou 20162 (K). Fig. B. Anemia glareosa. Gardner 4086 (K, type)

PLATE XVII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia brandegeea. Brandegee, 5 Nov. 1904 (GH, type) Fig. B. Anemia intermedia. Jones 23472 (UC, isotype).

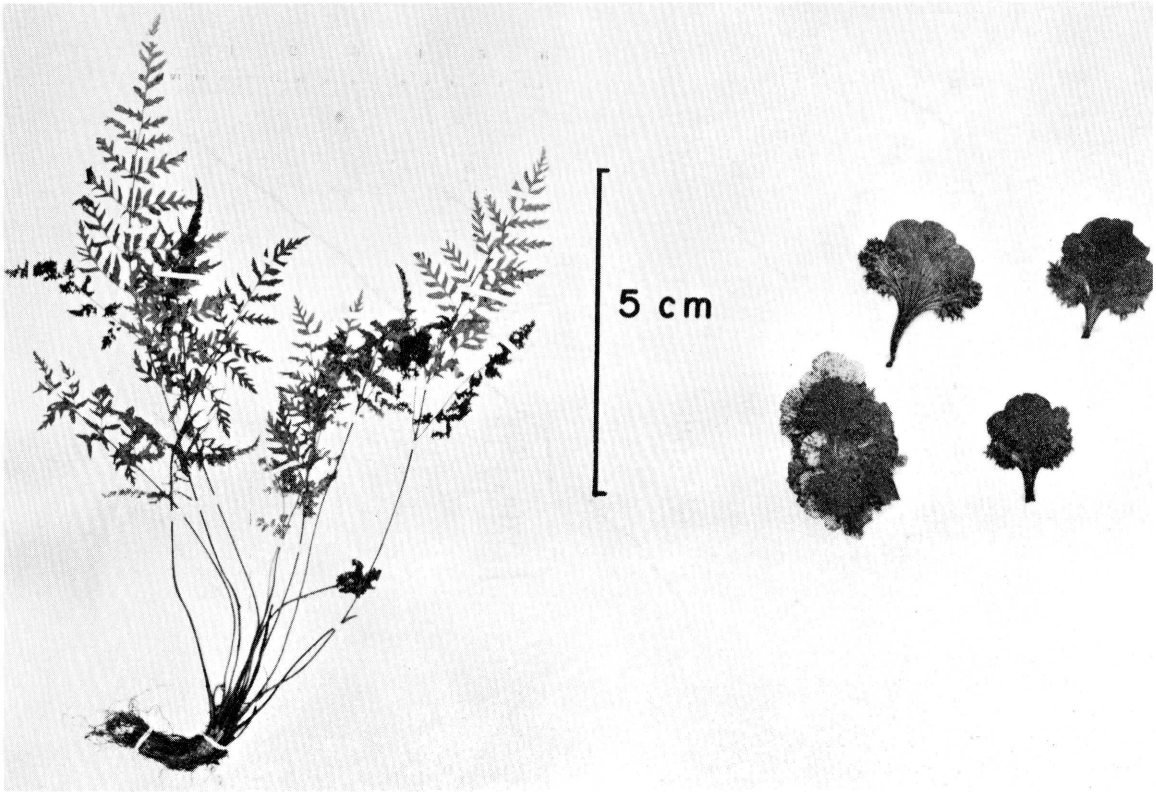


PLATE XVIII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia smithii. Fosberg 19475 (US). Fig. B. Anemia elegans. Damazio 1875 (NY).

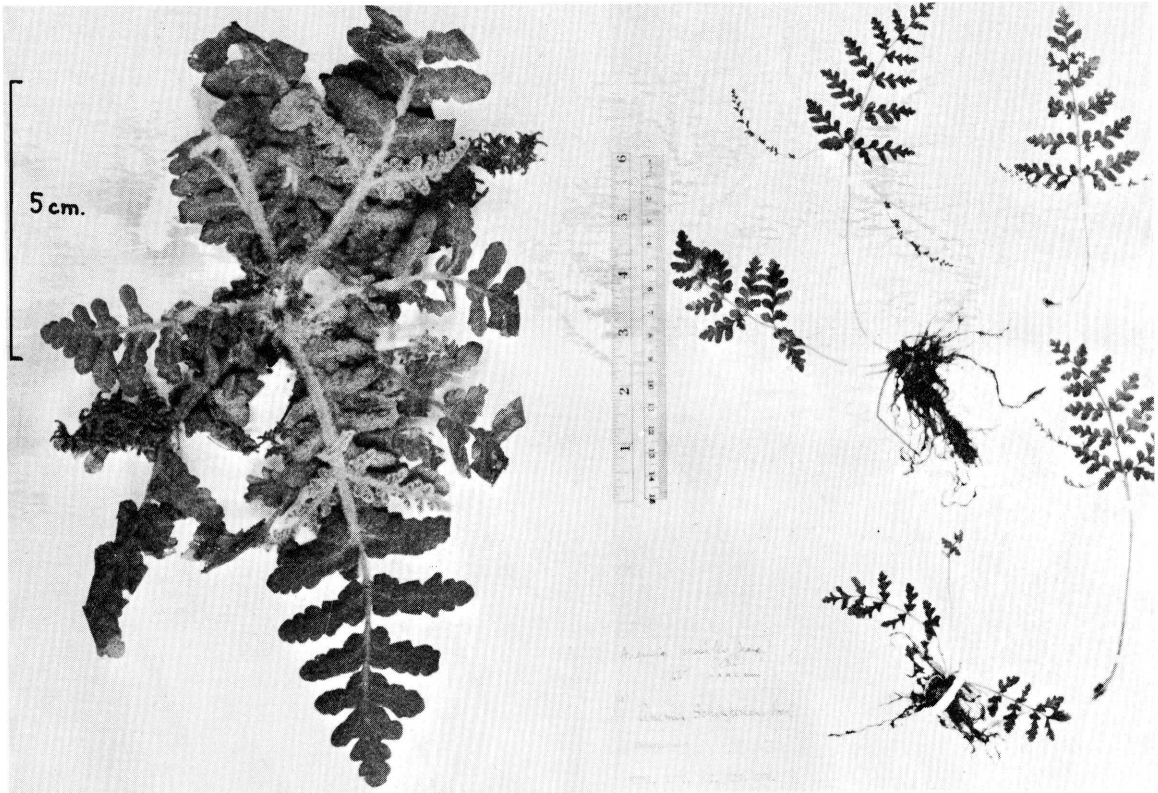


PLATE XIX. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia eximia. Ule 540 (R). Fig. B. Anemia sessilis. Lely 307 (K).

PLATE XX. Representative specimens of Anemia, subg. Coptophyllum

Fig. A. Anemia madagascariensis. Humbert 2857 (P, isotype)

Fig. B. Anemia schimperiana. Schimper 1203 (K, isotype).

PLATE XXI. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia aethiopica. Brockman 171 (K). Fig. B. Anemia wightiana. Lobb 39 (MO).

PLATE XXII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia simii. Johnson 180 (K). Fig. B. Anemia angolensis. Gossweiler 9705 (K).

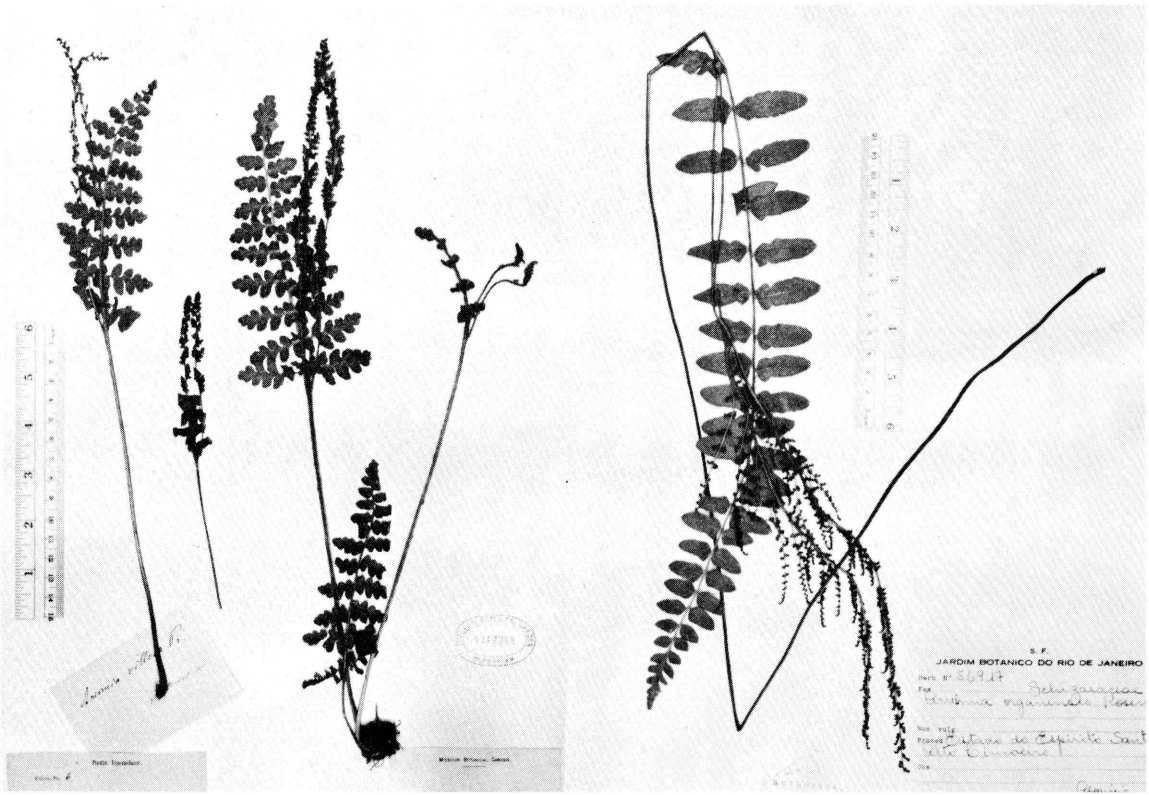


PLATE XXIII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia villosa. Fendler 6 (MO). Fig. B. Anemia organensis. Brade 18210 (NY).

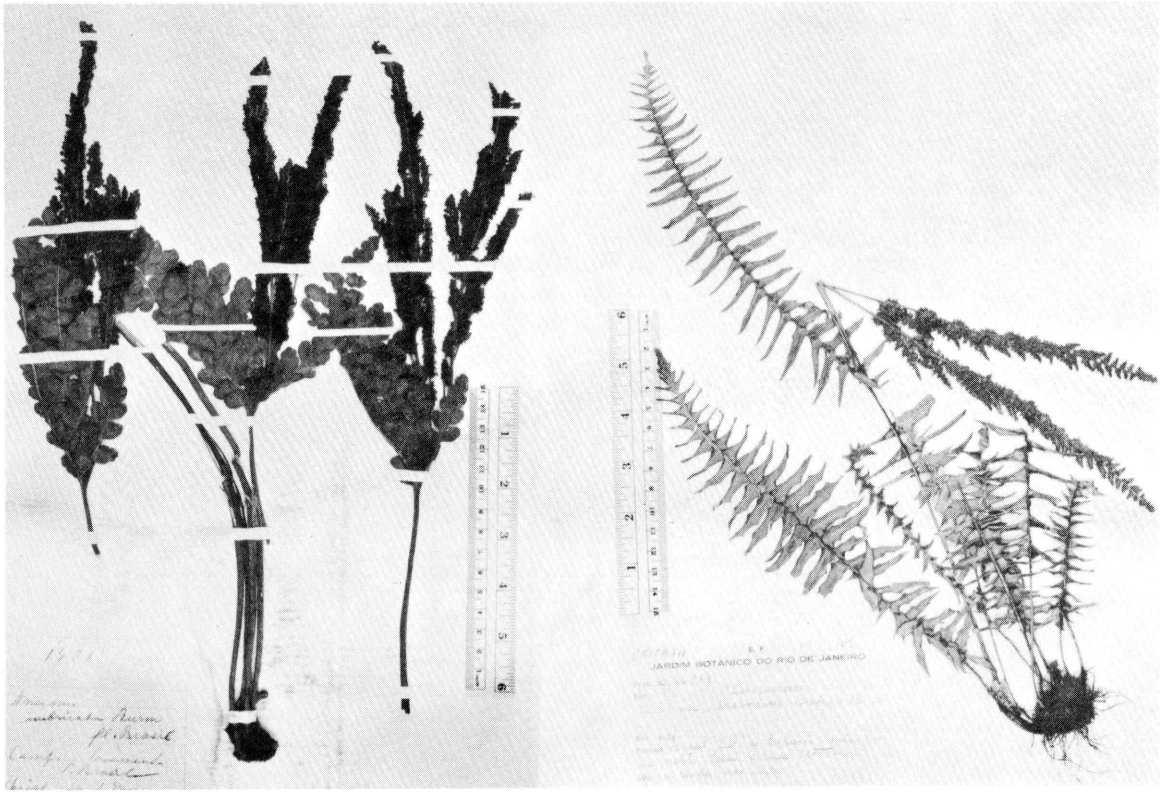


PLATE XXIV. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia imbricata. Damazio 1426 (MICH). Fig. B. Anemia blechnoides. Brade 19833 (RB, isotype).

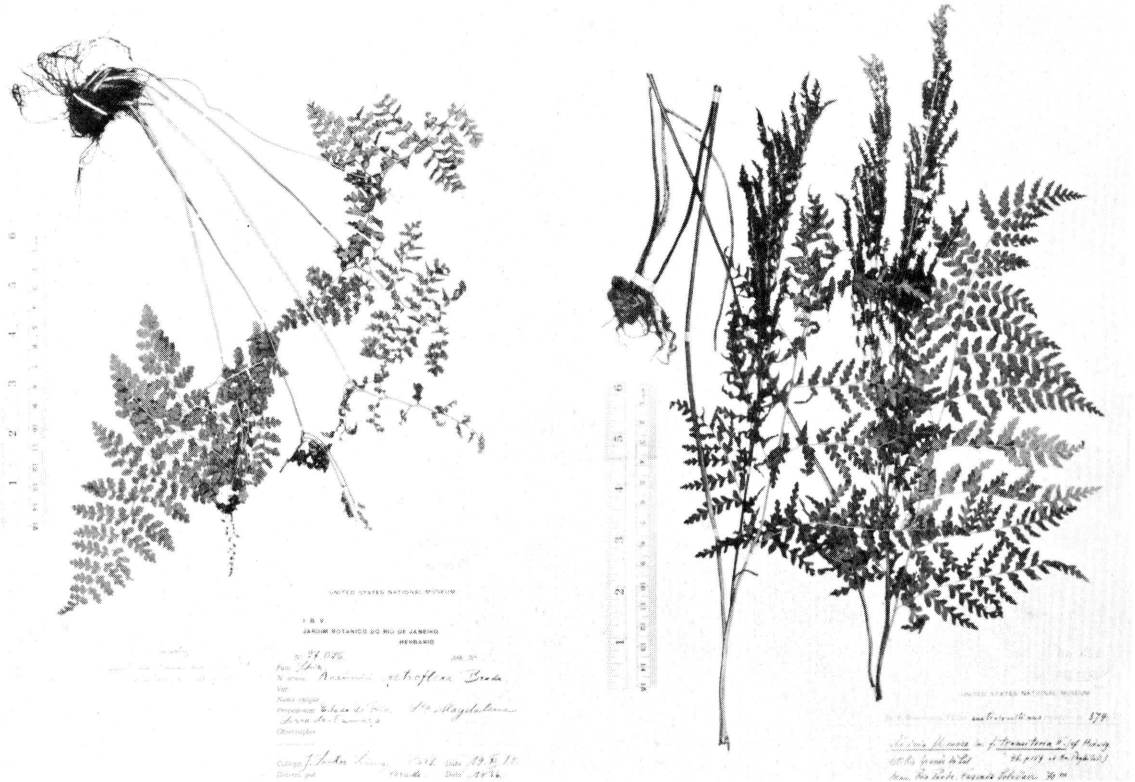


PLATE XXV. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia retroflexa. Santos Lima 328 (US, isotype). Fig.B. Anemia simplicior. Jurgens (Rosenstock

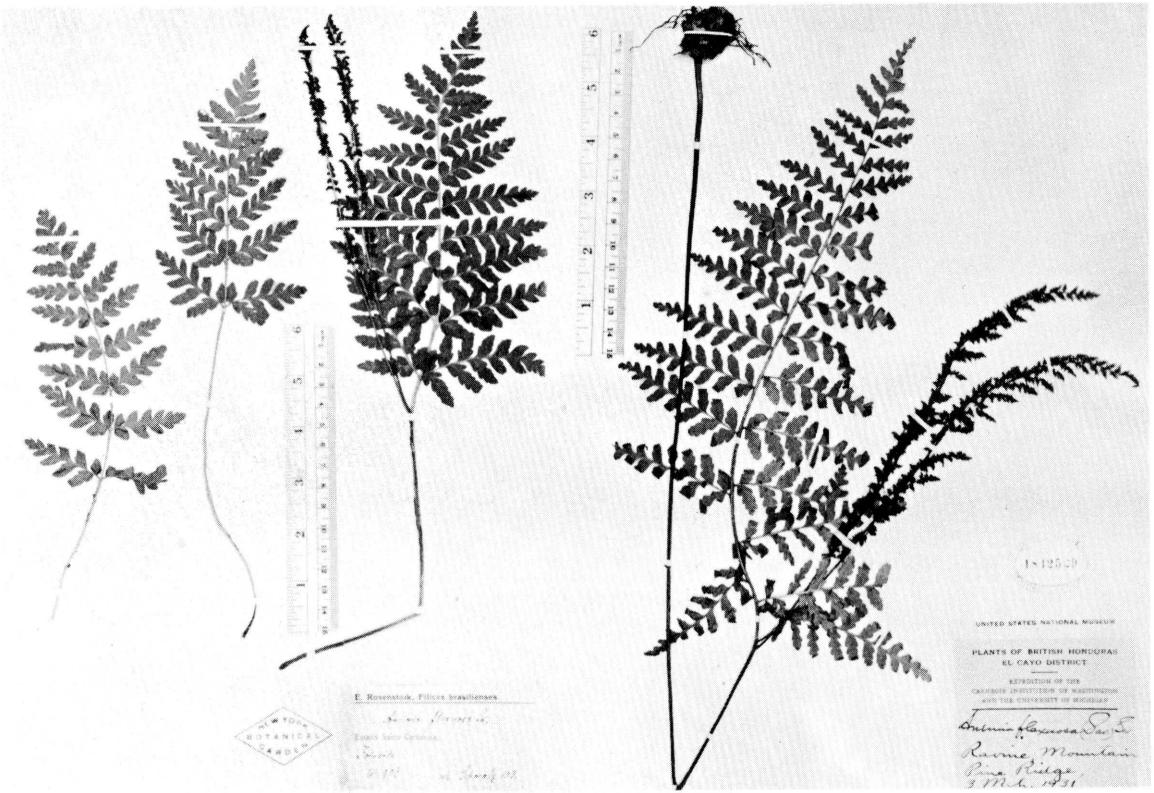


PLATE XXVI. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia raddiana. Schmalz 103 (NY). Fig. B. Anemia bartlettii. Bartlett 11898 (US, isotype).

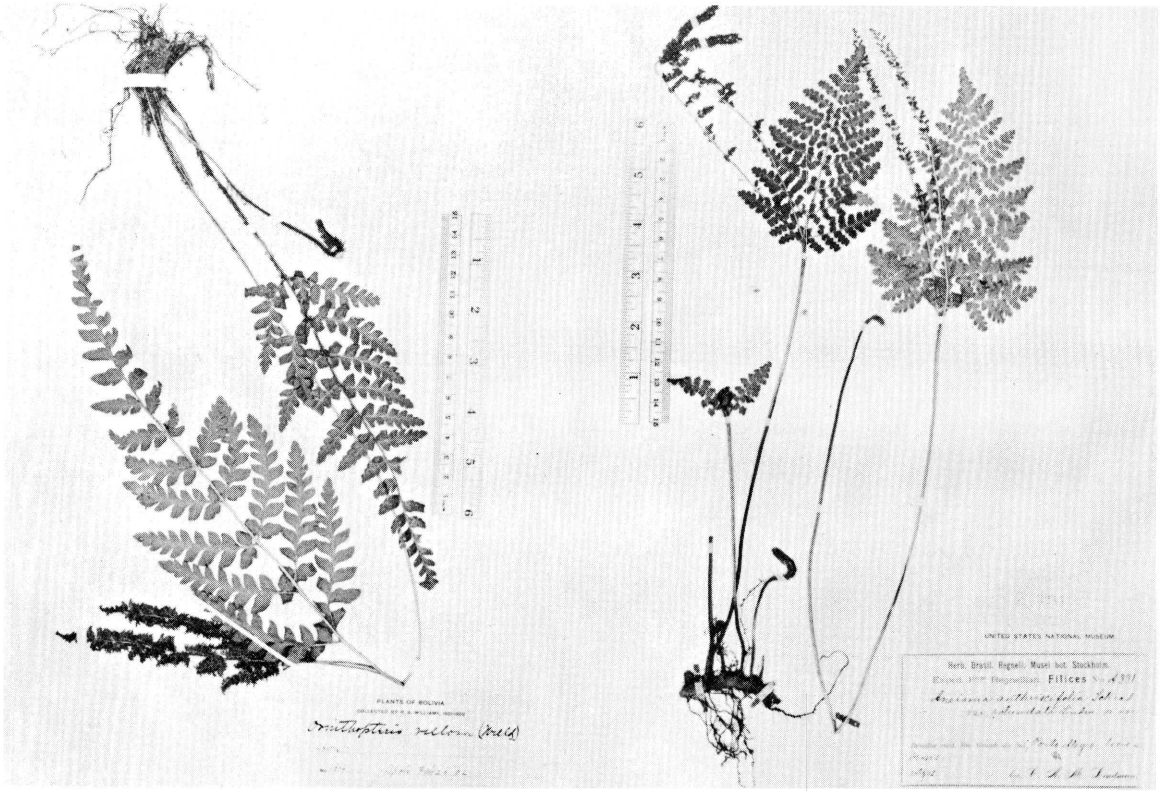


PLATE XXVII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia flexuosa. Williams 1364 (NY). Fig. B. Anemia tomentosa var. tomentosa. Lindman A331 (US).

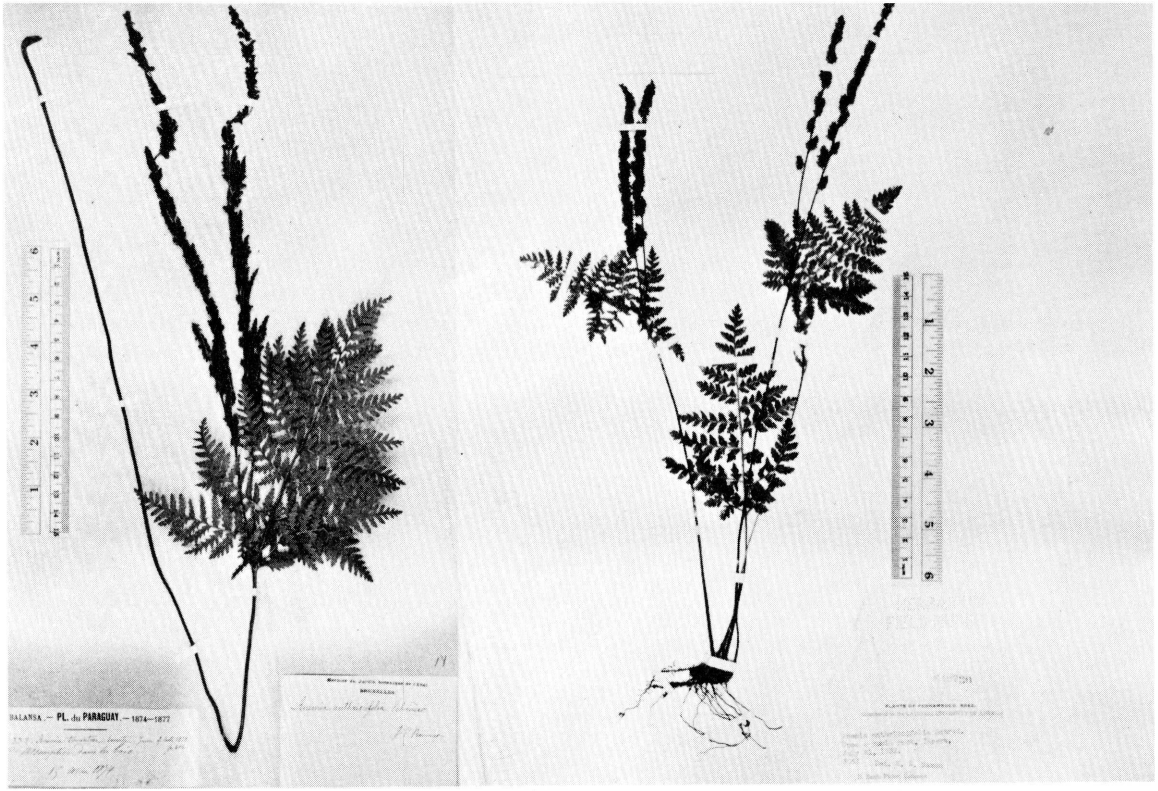


PLATE XXVIII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia tomentosa var. anthriscifolia. Balansa 332 (BR).
Fig. B. Anemia tomentosa var. anthriscifolia. Pickel 3053 (F).

PLATE XXIX. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia tomentosa var. australis. Abbiotti 1043 (US, type). Fig. B. Anemia tomentosa var. mexicana. Pringle 1834 (UC).

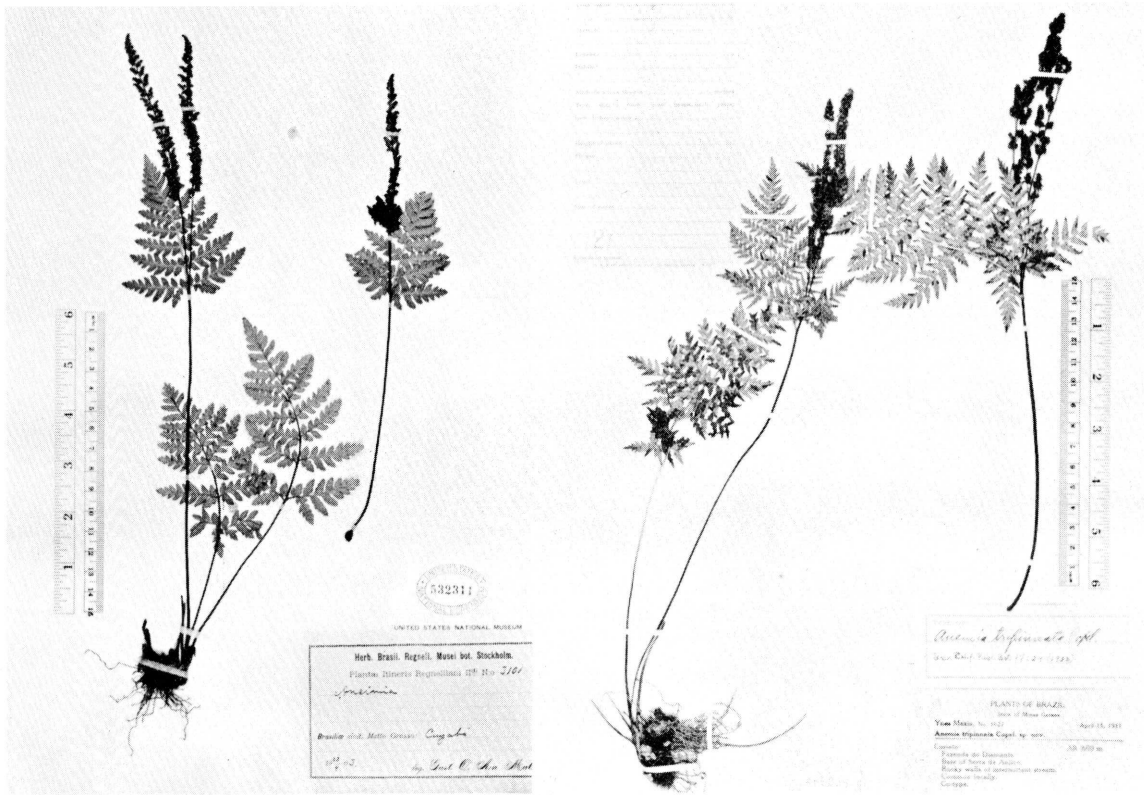


PLATE XXX. Representative specimens of Anemia, subg. Coptophyllum

Fig. A. Anemia ferruginea var. ferruginea. Malme 3101 (US).

Fig. B. Anemia ferruginea var. ahenobarba. Mexia 5627 (UC).

PLATE XXXI. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia myriophylla. Fiebrig 2541 (P, isotype). Fig. B. Anemia karwinskyana. Hinton 11338 (NY).

PLATE XXXII. Representative specimens of Anemia, subg. Coptophyllum
Fig. A. Anemia guatemalensis. Heyde and Lux (Donnell Smith 4095) (NY, isotype).
Fig. B. Anemia colimensis. McVaugh 15537 (MICH, type).

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GENETICS OF OAT STEM RUST RESISTANCE. I. INHERITANCE OF REACTION TO RACES 6, 8, AND 13A IN C.I. 3039[1]

J.A. Browning and K.J. Frey[2]

SUMMARY. Inheritance studies of crosses of C.I. 3039 with Markton, Richland, and Canuck have shown that C.I. 3039 possesses a single recessive gene pair for conditioning resistance to oat stem rust races 6, 8, and 13A. The C.I. 3039 gene is neither allelomorphic to nor linked with the B or the E genes.

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The discovery of C.I. 3039 as a possible new source of resistance to the common races 7, 7A, and 8 of the oat stem rust fungus (Puccinia graminis Pers. f. sp. avenae Eriks s. and E. Henn.) and to the rare races 6, 8A, and 13A was reported by Browning (2) and Browning and Frey (3). More recently, Green et al. (4) reported C.I. 3039 resistant also to stem rust races 1, 2, 6A, 10, and 13. For the most effective use of this source of resistance, its mode of inheritance must be known. Preliminary data (3) indicated that the resistance of C.I. 3039 to races 6, 7, and 8 was inherited as a recessive. This paper reports the mode of inheritance of the C.I. 3039 reaction to stem rust races 6, 8, and 13A in three oat crosses.

Materials and Methods

The oat strain C.I. 3039 was introduced into the United States from Africa as Selection No. 22 from the variety Kherson. For this study, C.I. 3039 was crossed with Markton (C.I. 2053), Richland (C.I. 787), and Canuck (C.I. 4024). The seedling stem rust reactions of these varieties are as follows: Markton is completely susceptible; Richland possesses stem rust resistance gene A (6) but is susceptible to races 6, 8, and 13A; Canuck has resistance gene B (5) which conditions a type-1 reaction to races 6 and 8, and gene E (5) which conditions a mesothetic reaction to race 13A; and C.I. 3039 gives a reaction of 2^{-}-2 to races 8 and 13A and of 2^{-}-2^{+} to race 6.

Inheritance studies were conducted using the F_1, F_3, and F_4 generations of Markton x C.I. 3039 and the F_2 and F_4 generations of Richland x C.I. 3039 and Canuck x C.I. 3039. The F_1 plants were tested by injecting

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[2] Associate Professor of Plant Pathology and Professor of Agronomy, respectively.

tillers in the three-leaf stage with spores suspended in a 0.5% solution of Tween-20[3]. Plants in the other generations were tested in the seedling stage by inoculating with talc suspensions of spores. Race 13A was used to establish the segregation ratio of F_2 seedlings and F_3 and F_4 lines, and races 6 and 8 were used to test F_4 lines to determine the association of reaction to race 13A and races 6 and 8. In the F_2 generation, 300 to 700 seedlings from a cross were classified for reaction to stem rust. The F_3 and F_4 generations were classified on a line basis, each line tracing to an F_2 plant. Each line was classified as homozygous resistant, segregating, or homozygous susceptible to a race on the basis of reaction of approximately 100 seedlings.

After inoculation with the talc suspension of spores, the seedlings were wet down with a 0.5% solution of Tween-20, kept in a moist chamber overnight, and subsequently maintained in the greenhouse at 60° to 70°F. The plants were classified for reaction to rust about 2 weeks after inoculation according to the system of Bailey (1). Infection types of 1, 2, and X⁻ were pooled as resistant and X, 3, and 4 were pooled as susceptible reactions except that for crosses involving Canuck, X-type reactions to race 13A were considered resistant.

Experimental Results

C.I. 3039 x Markton

Of the 10 F_1 plants of C.I. 3039 x Markton inoculated with races 6 and 8 of oat stem rust, nine were susceptible to race 6 and six were susceptible to race 8. Infection did not develop on the other F_1 plants. Since the resistant parent, C.I. 3039, was used as the female in this cross, the susceptible reaction of the F_1 plants indicated that susceptibility was dominant.

Sixty-two F_3 lines of C.I. 3039 x Markton were tested with race 8, and 200 F_4 lines were tested with race 13A. Each race gave a satisfactory fit to a ratio of 1 resistant: 2 segregating: 1 susceptible (Table 1), indicating that Markton and C.I. 3039 differed for reaction to stem rust races 8 and 13A by one gene pair.

Fifty of the F_4 lines tested with 13A were inoculated with races 6 and 8. In each line the reaction to race 6 and/or 8 was identical to the reaction to 13A (Table 2). These data show that the same gene pair conditioned reaction to the 3 races, 6, 8, and 13A, in this cross.

Richland x C.I. 3039

In Richland x C.I. 3039, the segregation of F_2 seedlings for reaction to race 13A gave a satisfactory fit to a ratio of 1 resistant: 3 susceptible (Table 3). These data corroborate the conclusion of Browning and Frey (3) that the resistant reaction of C.I. 3039 to oat stem rust is recessive to susceptibility. The 199 F_4 lines tested with race 13A gave a satisfactory fit (Table 3) to a ratio of 1 resistant: 2 segregating: 1 susceptible.

[3] The mention in this publication of a trade product, equipment or a commercial company does not imply its endorsement by the U. S. Department of Agriculture over similar products or companies not named.

Table 1. Observed and expected numbers of oat stem rust resistant, segregating, and susceptible F_3 and F_4 lines from Markton x C. I. 3039.

Race	Generation	Rust reaction	No. lines Obs.	No. lines Exp.	Chi^2	Probability
8	F_3	Res.	13	15.5[a]		
		Seg.	39	31.0	4.41	.20 - .10
		Sus.	10	15.5		
13A	F_4	Res.	52	50[a]		
		Seg.	105	100	1.31	.75 - .50
		Sus.	43	50		

[a] 1:2:1 ratio expected

Table 2. Reaction of F_4 lines from C.I. 3039 x Markton to stem rust races 6, 8, and 13A.

Race		13A		
	Reaction	Resistant	Segregating	Susceptible
6 and/ or 8	Resistant	22		
	Segregating		14	
	Susceptible			15

Table 3. Observed and expected numbers of oat stem rust resistant, segregating, and susceptible F_2 seedlings and F_4 lines from Richland x C.I. 3039.

Race	Generation	Rust reaction	No. lines Obs.	No. lines Exp.	Chi^2	Probability
13A	F_2	Res.	166	174[a]	0.49	.50 - .30
		Sus.	530	522		
	F_4	Res.	49	49[b]		
		Seg.	98	100	0.18	.95 - .90
		Sus.	52	49		

[a] 1:3 ratio expected
[b] 1:2:1 ratio expected

Reactions of the parental lines and of three representative lines from this cross to race 13A are shown in Fig. 1. Both the F_2 and F_4 generation data indicate that Richland and C.I. 3039 differ for reaction to race 13A by one gene pair also. Fifty of the F_4 lines which had been tested with race 13A were also inoculated with races 6 and 8. There was a perfect association between the reaction of the lines to race 13A and their reaction to races 6 and/or 8 (Table 4). Obviously, the same gene pair is involved in the inheritance of reaction to stem rust races 6, 8, and 13A.

Table 4. Reaction of F_4 lines from Richland x C. I. 3039 to oat stem rust races 6, 8, and 13A.

Race		13A		
	Reaction	Resistant	Segregating	Susceptible
6 and/ or 8	Resistant	17		
	Segregating		17	
	Susceptible			16

Canuck x C.I. 3039

The F_2 seedlings of Canuck x C.I. 3039 segregated 319 resistant to 64 susceptible which was a satisfactory fit to the ratio 13 resistant: 3 susceptible (Table 5). This ratio suggests that two gene pairs conditioned reaction to race 13A in this cross, one with resistance dominant and one with resistance recessive. The F_4 lines gave a ratio of 7 resistant: 8 heterozygous: 1 susceptible (Table 5) which corroborated the two-gene hypothesis suggested in the F_2 generation.

Table 5. Observed and expected numbers of oat stem rust resistant, segregating, and susceptible F_2 seedlings and F_4 lines from Canuck x C.I. 3039.

Race	Generation	Rust reaction	No. lines Obs.	No. lines Exp.	Chi^2	Probability
13A	F_2	Res.	319	311[a]	1.10	.50 - .25
		Sus.	64	72		
	F_4	Res.	81	88[b]		
		Seg.	108	100	1.30	.75 - .50
		Sus.	11	12		
6	F_4	Res.	36	35[b]		
		Seg.	40	39	.80	.95 - .50
		Sus.	3	5		

[a] 13:3 ratio expected
[b] 7:8:1 ratio expected

Figure 1. Reactions to oat stem rust race 13A of C.I. 3039, Richland, and homozygous resistant (-2-8), susceptible (-6-31) and segregating (-6-30) F_4 lines from the cross Richland x C.I. 2030.

F_4 lines of the cross Canuck x C.I. 3039 also gave a satisfactory fit to a segregation ratio of 7:8:1 when tested with race 6 (Table 5), also indicating that two gene pairs conditioned reaction to this race.

The genes segregating for reaction to races 6 and 13A presumably were the B and E genes from Canuck and the new gene from C.I. 3039. The E gene gave a mesothetic reaction to race 13A with resistance being dominant; the B gene conditioned a type 1 reaction to race 6 with resistance dominant; and C.I. 3039 gave a type 2 reaction to races 6 and 13A with resistance being recessive.

Discussion

Infection types which developed on C.I. 3039 in response to inoculation with oat stem rust races 6, 7, 7A, 8, and 8A (2, 3) indicated that C.I. 3039 was a new source of resistance to these races. C.I. 3039 was among eight oat lines first reported as being resistant to race 13A (2), all other lines being either susceptible or, if they contained the E gene, mesothetic in response to 13A. Thus the stem rust resistance gene (or genes) contained in C.I. 3039 was, of necessity, different from known genes A, B, D, and E although it (they) could have been allelomorphic to one of the known genes.

Inheritance studies reported herein have shown, however, that C.I. 3039 possesses a single gene pair for conditioning reaction to race 13A. When F_4 lines from the crosses, Markton x C.I. 3039 and Richland x C.I. 3039, were tested for reaction to races 6 and/or 8, their classifications were always identical to the classification for race 13A reaction. Obviously, the C.I. 3039 gene not only conditions resistance to race 13A but to key races 6 and 8 also.

The C.I. 3039 gene was inherited independently from the B and E genes in the Canuck cross, showing that it was neither allelomorphic to nor linked with the B or the E genes. However, genetic data are not yet available to show whether the C.I. 3039 gene is allelomorphic to the A or D genes. Contrary to previously described genes in which resistance is dominant, the C.I. 3039 gene is inherited as an incomplete recessive.

There are certain similarities between the effect of the stem rust resistance gene from C.I. 3039 and the "F" gene recently reported by Welsh *et al.* (5). Both are temperature sensitive, recessive, and inherited independently from the B gene, and both condition resistance to 13A. Crosses between C.I. 3039 and R.L. 524.1 (the source of the "F" gene) will be necessary to determine whether the two genes are the same. As a point of clarification, the gene from R.L. 524.1 should be designated "f" instead of "F," indicating that susceptibility is dominant, in accordance with the practice of designating dominant genes for oat stem rust reaction with capital letters.

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